FEMALE MOUNTING IN JAPANESE MACAQUES: PROXIMATE AND ULTIMATE PERSPECTIVES ON NON-CONCEPTIVE SEX

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ABSTRACT

Japanese macaques are unique in their sexual behaviour, adult females perform both female-female and female-male mounting. Female-male mounting is hypothesized to be adaptive, and female-female mounting is a functionless by-product of this adaptation. In this thesis, the proximate and ultimate forces behind both forms of mounting were explored using Eshkol-Wachman Movement Notation. In Chapter 2, the hypothesized adaptive value of female-male mounting was supported, as female-male mounts were related to greater subsequent male-female mounting. Additionally, the majority of female-male mounts were female-initiated, and males stood to be mounted in response to both ambiguous cues and explicit signals put out by females. In Chapter 3, the phylogenetic relatedness of female-male and female-female mounting was investigated by comparing the limb positions employed by mounters during both behaviours. Female-male and female-female mounters did not differ in the limb positions used during mounts, providing support for the hypothesized evolutionary link between the two.

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2.

CHAPTER 3.

LIST OF FIGURES

CHAPTER 3.

Introduction

Sexual behaviour is defined as the occurrence of mounting, courtship displays, solicitations, and interactions involving genital contact between two individuals (Vasey, 2007). While these behaviours are deemed to be sexual due to their strong relationship with the ultimate functional goal of reproduction, there are instances in which behaviours adhere to the general definition of "sexual" in almost every aspect, but do not have any direct effect on conception (Wundram, 1979). Non-conceptive sexual interactions can involve: (1) a non-oestrus female and a male, (2) a sexually immature individual and a sexually mature one, (3) two sexually immature individuals, and (4) same-sex individuals (Furuichi, Connor, & Hashimoto, 2014). Non-conceptive sexual interactions can also include non-reproductive insertive behaviours, such as oral and anal sex (Wundram, 1979).

Non-conceptive sex is a significant component of the behavioural repertoires of over 125 mammalian species (Dagg, 1984) and is especially common in primates (Furuichi, et al. 2014; Wallen, 2001). Across species, such behaviours are observed in a wide variety of contexts, such as social play, aggressive interactions, grooming interactions, stressful events, excitement stemming from an individual's own proceptive condition, and viewing the sexual activity of others (Dagg, 1984). With sex being unrestricted to reproduction and spilling over into other areas of animals' social lives, questions arise regarding the evolutionary history, adaptive function, and proximate mechanisms underlying non-conceptive sex. Specifically, how did such behaviours come about, why do they persist, and what triggers their occurrence?

In terms of non-conceptive sex, a nonhuman primate species that is of particular interest is the Japanese macaque (*Macaca fuscata*). First, from a developmental perspective, sexual interactions between immature individuals of both sexes commonly occur in this species in a variety of contexts (Gunst, Leca, & Vasey, 2013; Hanby, 1974; Hanby & Brown, 1974; Leca, Gunst, & Vasey, 2014a). Second, from an intergroup comparative perspective, some populations of Japanese macaques exhibit relatively high levels of female-female (Leca, Gunst, Ottenheimer Carrier, & Vasey, 2014b; Vasey, 2002a; Vasey & Duckworth, 2006;), male-male (Leca, Gunst, & Vasey, 2014c; Takenoshita, 1998), and female-male mounting (Gouzoules & Goy, 1983; Leca et al., 2014b; O'Neill, Fedigan, & Ziegler, 2004a; Vasey & Duckworth, 2008), as well as, masturbation in males (Thomsen & Soltis, 2004) and females (Wolfe, 1979a).

Among these sexual behaviours, female-female mounting and female-male mounting are especially interesting. Specifically, both occur within the context of temporarily exclusive sexual partnerships (i.e., consortships), and due to positional mechanics or biological unfeasibility, female-male and female-female mounting, respectively, do not directly result in conception. However, their occurrence in different social contexts suggests that female-male mounting may have indirect reproductive implications (Vasey, 2002b, 2006, 2007; Vasey & Duckworth, 2008), whereas female-female mounting does not. Given the similarities and differences in both forms of female mounting, the Japanese macaque is an exemplary model species to study the evolutionary history and function of non-conceptive sex.

Japanese Macaque Ecology and Sexual Behaviour

The Japanese macaque is a species of short-tailed monkey that is native to the archipelagic nation of Japan. It is the northernmost-living non-human primate and is widespread across Japan, with their geographic distribution ranging from the north point of the country's largest island of Honshu (41°30'N) to the southern island of Yakushima (30°15'N) (Fooden & Aimi, 2005). Japanese macaque females are philopatric, remaining in their natal groups and maintaining stable social bonds with female kin. In contrast, males disperse from their birth troop before reaching full sexual maturity (Fooden & Aimi, 2005; Fukuda, 2004). Japanese macaque social structure is characterized by a linear matrilineal dominance hierarchy, with troops being composed of multiple matrilines whose adult female and subadult members share a collective rank, resulting in female bloodlines being dominant or subordinate relative to one another (e.g. matriline A outranks matriline B, which outranks matriline C) (Koyama, 1967). Individuals within matrilines also rank differentially, with sisters ranking in reverse order of age (Kawamura, 1958; Koyama, 2003). Like other macaque species, Japanese macaques employ a multimale-multifemale mating system (Dixson, 2012).

Reproduction and sexual behaviour in Japanese macaques occur exclusively during the fall-winter mating season, which lasts from the months of October to February (Fooden & Aimi, 2005). During this time, adolescent and adult individuals exhibit reddening of the skin around the face, genital area, and nipples (Fooden & Aimi, 2005). In females, oestrus level appears to be related to skin redness (Nigi, 1975) and this reddening of skin is cyclical throughout the mating season (Takahata, 1980). Interestingly, the level of sexual motivation does not seem to be governed completely by

ovulatory hormone levels, as females engage in sexual behaviour during both the fertile and non-fertile phases of their menstrual cycles (Fedigan & Gouzoules, 1978; Gouzoules & Goy, 1983; O'Neill et al., 2004a, O'Neill, Fedigan, & Ziegler, 2004b). Throughout the mating season, sexually motivated individuals form temporary but exclusive non-kin dyads called consortships, during which the partners partake in synchronized and reciprocal behaviours, such as grooming, huddling, following, and feeding (Gouzoules & Goy, 1983; Wolfe, 1986). In addition to this, the consorting partners engage in sexual behaviours such as series mounting, as well as postural, vocal, and facial solicitations (Vasey, Chapais, & Gauthier, 1998).

Female-Female Mounting in Japanese Macaques

The earliest investigations into homosexual behaviour in primates, suggested that same-sex sexual interactions were solely the product of abnormal conditions, such as captivity and hormonal imbalance (see Vasey, 1995). However, such behaviour is now known to routinely occur between conspecifics with sex- and species-typical physiology, as well as those that are living in species-typical environmental and social conditions (Vasey, 2002a). Therefore, in the majority of cases, atypical conditions cannot explain the occurrence of homosexual behaviour in wild animals, but rather, its persistence must be driven by evolutionary forces and thus explainable in evolutionary terms (Vasey, 1995). Such is the case for female Japanese macaques, which exhibit same-sex mounting in captive, free-ranging, provisioned and non-provisioned troops. As such, female homosexual behaviour can be accurately described as part of this species' typical repertoire of sexual behaviour in some populations (Takahata, 1980).

The sexual nature of female-female mounting. While courtship displays,

mounting, and genital contact are typically exhibited in the context of heterosexual

interactions, they also routinely occur between same-sex partners in a variety of primate

species, such as bonobos (*Pan paniscus*), guinea baboons (*Papio papio*), and Hanuman

langurs (*Semnopithecus ajax*) (Dixson, 2012). Much of the literature in the field of

animal behaviour categorizes homosexual behaviour as being socio-sexual in nature

(Bagemihl, 1999), with its outward sexual form acting as a means to attain a particular

adaptive breeding strategy or social goal (Dixson, 2012; Vasey & Sommer, 2006;

Wickler, 1967). Genito-genital rubbing between female bonobos, for example, may be

performed during feeding to reduce tension (Fruth & Hohmann, 2006). In Japanese

macaques, however, female homosexual mounting does not lend itself well to a

sociosexual interpretation. In fact, over four decades of research on specific Japanese

macaque populations, such as the Arashiyama-E troop in Kyoto (Huffman, Fedigan,

Vasey, & Leca, 2012), have found no relationship between this behaviour and ulterior

social goals (see Vasey, 2004a). As outlined by Vasey (2006, 2007), female-female

mounting in Japanese macaques has *not* been found to facilitate any of the following

social goals: to establish alliances with non-kin females outside of consortships (Vasey,

1996), to communicate hierarchical rank relative to one another (Vasey et al., 1998), to

obtain allo-parental care from their same-sex partners (Vasey, 1998), as a means of

reconciliation proceeding intra-dyad conflict (Vasey, 2004b), to reduce tension prior to

aggression (Vasey et al., 1998), or to function as practice for mounting males (Vasey,

2004b). In terms of heterosexual breeding strategies, female-female mounting has not

been found to sexually attract male partners (Gouzoules & Goy, 1983; Vasey, 1996,

1998; Wolfe, 1984), or to hinder the copulatory success of other females (Gouzoules & Goy, 1983).

If female-female mounting does not have an ultimate social function, then what is driving the routine occurrence of this behaviour in some Japanese macaque populations? Many lines of evidence converge to offer one answer: that homosexual mounting in this species is a purely sexual behaviour, adhering to the definition of "sex" in every manner except for its lack of direct reproductive benefits. As outlined by Vasey (2006, 2007) and Wolfe (1986), three pillars of evidence support this notion. First, same-sex sexual interactions bear a striking resemblance to heterosexual copulation and courtship in five distinct ways: (1) as is typical of male-female mounting, females of this species only mount one another during the fall-winter mating season; (2) the consortships they form with their female mounting partners are characterized by the same activities and behaviours that define heterosexual consortships, including bidirectional solicitations and synchronized social activities; (3) there is a mutual sexual attraction between female mounters, as they mount one another in a bi-directional manner, do not attempt to remove their same-sex partners during mounts, and often grab their partner as they are being mounted; (4) homosexually-consorting females are sexually receptive, as signalled by their reddened faces and perinea; and (5) some ways in which females mount one another bears structural similarity to heterosexual male mounting (i.e.,double foot-clasp mounts).

Second, the relationship between homosexual mounting partners is radically distinct from regular social interactions, suggesting that they are purely sexual in nature. For example, females do not form homosexual consortships with close female kin (e.g., mother, sisters, grandmothers; Chapais, Gauthier, Prud'homme, & Vasey, 1997; Chapais

& Mignault, 1991; Gunst, Leca, & Vasey, 2015). In the context of homosexual consortships, females spend the majority of their time within proximity of their same-sex partners (Gouzoules & Goy, 1983; Vasey, 1996, 1998; Wolfe, 1984), defend one another during conflicts with other conspecifics (including their own kin) (Vasey, 1996), and grooming occurs more often *down* the hierarchy (i.e., subordinate consort partners receiving grooming from their dominant partners more often than the reverse) (Vasey, 1996). Such behaviours rarely occur outside of consortship contexts. Outside of consortships, females engage in affiliative behaviour with their female kin (e.g. grooming, conflict support), spend most of their time in proximity to close kin (Gouzoules & Goy, 1983; Vasey, 1996; 1998), do not defend non-kin during conflicts (Vasey, 1996), and groom *up* the dominance hierarchy (Chapais, Gauthier, & Prud'homme, 1995; Vasey, 1996).

Lastly, and importantly, sexual reward appears to be the proximate motivator for female-female mounting in this species. As described by Vasey and Duckworth (2006), the majority of female homosexual mounts include direct stimulation of the mounter's vaginal-perineal-anal (VPA) region. Mounters stimulate their VPA region by rubbing the area against the mountee's back/rump thereby affording both individuals with sexual stimulation. Mounters also use tail movements to stimulate their VPA region in ways that are unique to consortships and not observed during other social activities (Vasey & Duckworth, 2006). Tail movement and thrusting are also dissociable, which suggests that both actions are voluntary and thus carried out with a purpose (Vasey & Duckworth, 2006). Since the VPA region's main function is to receive erotic stimuli, provide sexual pleasure, and mediate sexual arousal (Dixson, 2012), and numerous sociosexual functions

for this behaviour have been disproven, it is likely that proximate sexual reward is a driving force underlying female-female mounting (Vasey & Duckworth, 2006).

Homosexual mounting as female-typical behaviour. Sexual behaviour is a highly dimorphic aspect of many animals' behavioural repertoires (Baum, 1979). This differentiation between the sexes is largely due to the sex-specific organization of neuroanatomical structures prenatally and the activation of neural mechanisms via differential exposure to sex steroid hormones (i.e. androgens and estrogens) during puberty (Adkins-Regan, 1988; Vasey & Pfaus, 2005). By the same token, by being exposed to sex-atypical hormones, individuals are likely to develop sex-atypical neuroanatomy and neurophysiology, and therefore, express sex-atypical behaviour (Adkins-Regan, 1988; Vasey & Pfaus, 2005). Since female Japanese macaques partake in homosexual behaviours, it is logical to contemplate whether their tendency to engage in same-sex mounting is associated with male-typical neuroanatomy, male-typical hormone exposure, or other male-typical behaviours.

Homosexual behaviour in female Japanese macaques is not governed by male-typical neuroanatomy. In a study by Vasey and Pfaus (2005), the anterior hypothalamic nucleus of the medial pre-optic area (MPO-AH) of unmanipulated males and females from a population in which homosexual mounting occurs were compared. This brain area, which is known to regulate sexual behaviour in primates (e.g. Kendrick & Dixson, 1986), was found to be female-typical in size and not "masculinized" in any way. Interestingly, studies done on the size of comparable homologous nuclei in other species (e.g. humans (*Homo sapiens*): Byne et al., 2001; domestic sheep (*Ovis aries*): Roselli, Larkin, & Resko, Stellflug, & Stormshak, 2004) have found that these structures are sex-

atypical in males that exhibit exclusive same-sex sexual attraction. In a study by Eaton, Worlein, Martin, & Glick (1988), 80% of the adult female sample were never observed performing same-sex mounts, despite having been exposed to androgens prenatally. Studies on the effects of brain anatomy and prenatal hormones on homosexual female mounting in Japanese macaques have been few and more research is needed to understand the role that both play in the expression of homosexual mounting in female Japanese macaques.

Mounting is a male-typical behaviour in the majority of species (Baum, 1979). Although female Japanese macaques mount, the overall *manner* in which females engage in mounting and related sexual behaviours generally cannot be characterized as masculine. First, the strategies females use to attain and maintain female consort partners are, for the most part, female-typical. Unlike males, females rarely perform consortship intrusions, and when they do, the level of harassment and sexual coercion they exhibit are significantly lower than male-typical rates (Vasey, 2004a). Females do, however, aggress third-party males who attempt to gain access to their same-sex consort partners (Vasey, 2004a).

Second, female-female mounting is characterized by a greater level of variety than heterosexual male mounting. While males almost exclusively employ thrusting double foot-clasp mounts, females perform a much wider variety of mounts types, including: double foot-clasp mounts with and without thrusting, reclining mounts without thrusting, and sitting mounts with and without thrusting (Vasey, Foroud, Duckworth, & Kovacovsky, 2006). Given that double foot-clasp mounting with thrusting is the only mount that is commonly exhibited by both male and female mounters, Vasey et al. (2006)

found that the movements involved in female-female mounting were very distinct from, and not typical of, heterosexual male mounts. Compared to males, homosexual female mounters incorporated more pelvic movement, as well as a much wider variety of movement types (Vasey et al., 2006). The movements that females employed were also significantly more complex than those of males, who, unlike females, were never observed to simultaneously combine different movement types (Vasey et al., 2006). Females were also described as being more continuous and fluid in their pelvic movements, while male thrusting incorporated more "clear and precise movements" (Vasey et al., 2006 p. 127).

While it can be said that the physical manner in which females mount is not masculine and thus "female-typical", the structural difference in mounts performed by both sexes is likely due to their differences in sex-specific genital architecture. Specifically, males are constrained due to the kinetic specificity required for penile-vaginal penetration, which is achieved most efficiently by double foot-clasp mounts and a rigid combination of precise movements (Vasey et al., 2006). In contrast, female VPA stimulation can be achieved and maximized using a large variety of mount types and movements. Moreover, unlike males, VPA stimulation by females is not constrained by the need for direct contact with their partner's body, as they also use their tails as stimulatory tools (Vasey & Duckworth, 2006; Vasey et al., 2008).

Skewed sex ratios and sexual partner preference in female Japanese macaques. Up to this point, it has been made clear that sexual behaviours and interactions between Japanese macaque females are not sociosexual, likely driven by proximate sexual reward, and, for the most part, not masculine in expression. Knowing

this, it is appropriate to ask if more immediate, proximate motivators drive female-female mounting, as well as how these factors potentiate females to engage in same-sex mounting, particularly when opposite-sex (and thus, theoretically preferable) partners are available.

On the surface, it is plausible to consider that female-female mounting is perpetuated by a particular aspect of group demography. Specifically, a female-skewed operational sex ratio, translating to a lack of reproductively available males relative to reproductively available females, has been found to be correlated with an elevated frequency of female-female mounting in Japanese macaques (Vasey & Gauthier, 2000; Wolfe, 1984; 1986). Upon closer inspection, however, "heterosexual deprivation" only offers a partial explanation for the occurrence of female-female mounting (Leca, Gunst, Huffman, & Vasey, 2015; Vasey, 2002b). An experimental study showed that when all but one male was removed from a captive group of Japanese macaques held at the Université de Montréal, females often rejected the solicitations of the sole male–an individual with whom most females had been sexually active at some point in the past– and opted to consort with same-sex individuals instead (Vasey & Gauthier, 2000). The fact that these females were exposed to a male that was (1) sexually proceptive, and (2) an acceptable mate (judging from past sexual interactions), therefore, does not support the view that male scarcity, *per se*, prompts female-female mounting, as females mostly chose to consort with females and rejected the available male. In light of this, it has been proposed that females likely have a *preference* for *certain* female and male consort partners, and an abundance of the former combined with the relative scarcity of the latter causes female-female sexual activity to increase in demographic conditions characterized

by female-skewed sex ratios (Vasey & Gauthier, 2000). Additional research indicates that females often exhibit a preference for female sexual partners when faced with a simultaneous choice between a male and female. Specifically, females that were the focus of simultaneous female-male competition (i.e. solicited by a male while in a homosexual consortship) overwhelmingly chose to remain with their female partner rather than joining the male to form a heterosexual consortship (Vasey, 1998).

In light of these findings, can it be said that female Japanese macaques have a homosexual partner preference? Yes and no. While it is true that females show a preference for *certain* same-sex partners in some populations, it is incorrect to consider them exclusively or preferentially homosexual, as they do so in combination with heterosexual behaviour, sometimes partaking in both within the same day (Vasey, 2002b). Although it is possible that some females are homosexually-inclined throughout a whole mating season (Vasey, 2002b), a recent longitudinal study of the Arashiyama-E troop showed that higher ratios of *preferred* female partners to preferred male partners were associated with female homosexual consortships rather than female heterosexual consortships (Leca et al., 2015). This result supports the "bisexual preference hypothesis", holding that female homosexual behaviour is attributed to female preference for certain female mates relative to certain male mates. Overall, female Japanese macaques are best characterized as exhibiting facultative same-sex sexual partner preference, but having a bisexual orientation (Vasey, 2002b).

Female-Male Mounting in Japanese Macaques

Unlike female-female mounting, female-male mounting in Japanese macaques has received significantly less attention in the literature. However, attempts have been

made to explain the occurrence of female-male mounting in animals, and some of these hypotheses have been applied to Japanese macaques in some manner. Morris (1955) proposed that animals' principal drives are inherently sex-specific and reflective of dominance status, with attacking being male-typical and characteristic of dominant individuals, and fleeing being female-typical and characteristic of subordinate individuals. According to Morris (1955), during copulation, the drives to attack and flee are expressed in the form mounting and allowing oneself to being mounted, respectively. This was thought to result in dominant and aggressive females engaging in "pseudomale" mounting when in the presence of an atypically submissive male, who responds in a "pseudofemale" manner by allowing themselves to be mounted. From a more functional point of view, Beach (1968, 1976; see also Ford & Beach, 1951) claimed that female-male mounting is proceptive behaviour that females employ towards sexually sluggish males. Specifically, a male subjected to female mounting should be sexually aroused by the act and subsequently prompted to mount the female in return (Beach, 1968, 1976). Since then, some primate researchers have referred to female-male mounting as a sexually proceptive behaviour (see Dixson, 2012; O'Neill et al., 2004a,). However, the *capacity* in which it promotes sexual interactions with males has yet to be empirically tested.

Morris' hypothesis has been deemed to lack overall conceptual and neurophysiological evidence (see Baerends, 1975; Gouzoules & Goy, 1983), and it is especially unclear as to how individuals' predispositions to attack and flee directly relate to mounting and being mounted, respectively. On the other hand, there is informal observational evidence which suggests that Beach's claim (1968, 1976) may be

appropriate for explaining female-male mounting in Japanese macaques. First, females of this species are known to place their hands on the hindquarters of their male consort partners, often followed by the female mounting and pelvic thrusting upon the male, who is often observed responding to these acts by mounting the female (Gouzoules & Goy, 1983; Vasey, 2002a). Second, females have also been observed soliciting mounts from, and mounting, their male consort partners upon males' movement away from their general vicinity (Vasey, 2002a). Therefore, it is suggested that female-male mounting in Japanese macaques is adaptive in nature, with sexually motivated females using this manoeuvre to restrict males' movement and stimulate sexually sluggish or distracted males, ultimately prompting males to partake in copulation and increasing chances of conception (VanderLaan, Pellis, & Vasey, 2012; Vasey, 2002a, 2006, 2007), otherwise known as the "proceptivity hypothesis".

Aside from the possible functional aspects of this non-conceptive sexual behaviour, female-male mounting may also be partially driven by proximate, pleasure-seeking motivations. Vasey and Duckworth (2008) found that two-thirds of females performing female-male mounting incorporated some form of VPA stimulation. Collectively, approximately half of all of these females' mounts involved VPA stimulation (Vasey & Duckworth, 2008). Analogous to what has been reported for female-female mounting (Vasey & Duckworth, 2006), females performing female-male mounting also achieved genital stimulation by pelvic thrusts and clitoral rubbing via hooking and sweeping tail motions. Pelvic thrusting and tail movement were sometimes dissociated from one another and thus each could be performed in a voluntary manner

(Vasey & Duckworth, 2008). Therefore, it seems safe to presume that female-male mounting is at least partly motivated by sexual reward.

The Evolutionary Link between Female-Male and Female-Female Mounting

To reiterate, female Japanese macaques' ability to perform both same-sex and opposite-sex mounts makes them ideal models to study the evolutionary basis for non-conceptive sex. To gain a full understanding of these behaviours, their adaptive function (i.e. why does the behaviour persist) *and* their evolutionary history (i.e. how did the behaviour come to be) must be taken into consideration (Gould, 1986; Vasey, 2007).

A behaviour may persist because it holds an adaptive value, having been naturally selected due to its facilitating effects on survival or reproduction (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). It seems that this explanation could fit female-male mounting in Japanese macaques, as this behaviour may function to sexually arouse males, prompt males to mount, and focus the male's attention on the consortship at hand (Vasey, 2002a, 2006, 2007). In contrast, despite extensive investigation, female-female mounting does not appear to have any adaptive function. Instead, it has been suggested that female-female mounting is a *by-product of an adaptation,* with female-male mounting being the adaptive basis to which female-female mounting is linked (VanderLaan et al., 2012; Vasey, 2002a, 2006, 2007). An evolutionary by-product is a characteristic whose existence and persistence is solely due to being coupled or "carried along" with an adaptation, even though it does not possess any fitness-enhancing value (Buss et al., 1998). The notion that female-female mounting in Japanese macaques is a by-product of female-male mounting is supported by a recent study that compared 14 different groups of Japanese macaques. This study showed that Japanese macaque

15

populations exhibit either: (1) no female mounting behaviour, (2) female-male mounting only, or (3) both female-female and female-male mounting behaviours. No groups were found to exhibit female-female mounting in the absence of female-male mounting. Taken together, this suggests that female-female mounting did not evolve in the absence of the purportedly adaptive precursor, female-male mounting (Leca, et al., 2014b).

To truly understand the evolution of a behaviour, particularly a seemingly functionless one like female-female mounting, evolutionary history must be taken into account. To this end, Vasey (2002a, 2006, 2007; see also VanderLaan et al., 2012) has proposed a four-stage model of the evolutionary development of female mounting in Japanese macaques. This model holds that: (1) during rough-and-tumble play, juvenile males engage in mounting interactions with their playmates (Hanby, 1974; Hanby & Brown, 1974; Gunst et al., 2013). Many of these mounts and mounting attempts involve the mountee turning around and directing its attention to the mounter. In other words, mounting prompts attention from the mountee. (2) Females were then able to exploit this male response by evolving the adaptive female-male mounting, which functions to focus male attention and prompt males to mount females in return. (3) Eventually, females evolved the ability to obtain proximate sexual reward while performing this female-male behaviour via thrusting and tail movement (Vasey & Duckworth, 2008). (4) Once females were able to mount and derive sexual gratification during female-male mounting, genital stimulation could have been achieved just as easily by mounting females instead of males. Consequently, at this point in the species evolutionary history, females would have begun to mount females not because it was functional, but because it was sexually rewarding. Subsequently, females may have begun preferring certain same-sex sexual

16

partners over males simply because the former were more sexually rewarding than the later (Vasey, 2002b). This could be due to the wide range of movements and mount types that females employ (Vasey et al., 2006), which likely afford them more direct VPA stimulation than intromission. Additionally, female-female mounting appears to be a "safer" alternative to heterosexual interactions, with homosexually consorting adolescent females being less likely to be aggressed and injured (Leca et al., 2014d). These reasons may explain why female sexual partners are sometimes chosen over male ones.

While the different stages of this parsimonious evolutionary scenario, including hypothesized mechanisms, functions and timeline, are, to some extent, consistent with available findings, further research is required to solidify its validity. This is particularly the case for Step 2 of the model, which relies heavily on anecdotal evidence. In this thesis, I will investigate the proximate mechanisms, functional significance, and evolutionary history of female mounting behaviour. This will largely be done using the Eshkol-Wachman Movement Notation (EWMN). EWMN is a globographic referencing system that quantifies an individual's positions and movements relative to themselves and others (Eshkol & Wachman, 1958). In Chapter 2, I will investigate both the proximate mechanisms and the adaptive function of female-male mounting. By quantifying male and female consort partners' physical movements and relative positioning before, during, and after the occurrence of female-male mounts via partner-wise EWMN, I aim to explore the behavioural correlates of both female-male and male-female mounting. Female-male mounting's function will be tested by quantifying the rate and likelihood of male-female mounting's occurrence subsequent to female-male mounting. In Chapter 3, I will explore the nature of the phylogenetic link between female-male and female-female

mounting by investigating the physical, structural similarity between both forms of mounting. To do so, I will compare the limb positioning of female mounters during both forms of mounting. The overarching goal of this research is to obtain a better understanding of the mechanisms and evolution of non-conceptive female mounting behaviour in Japanese macaques.

CHAPTER TWO

The Proximate Mechanisms and Ultimate Function of Female-Male Mounting

Abstract

It is hypothesized that female-male mounting is an adaptive behaviour, functioning to prompt sluggish males to mount females in return. This hypothesis has been proposed many times and independently by different authors, however it had yet to be tested. Furthermore, the proximate mechanisms that drive the behaviour, specifically the male and female movements and actions that prompt its occurrence, are relatively unknown, having only been reported in an anecdotal sense. In this chapter, I investigated both the adaptive function and proximate mechanisms that drive female-male mounting. In accordance with the "proceptivity hypothesis", I predicted that female-male mounting should be related to both an increase likelihood of occurrence and an increased frequency of subsequent male-female mounting, As for proximate mechanisms, I found that females were the initiators of female-male mounting during 79% of observed mounts. Furthermore, males were found to rise to be mounted in response to both ambiguous cues (i.e. females moving their bodies to position themselves into the mounter position) and explicit signals (i.e. females grasping the males' hindquarters) emitted by females initiating and carrying out the female-male mounting process. These results suggest that males anticipate and facilitate female-male mounting.

Introduction

The long-standing stereotype of female and male roles during heterosexual mating is that of an active male and a passive female, with males being portrayed as the sole initiators of sexual behaviours, and females being described as "reluctant" (Fedigan, 1982, p. 144) or passive when targeted with sexual advances (Beach, 1976). However, cross-species analyses, and more specifically, primate research, show that females do initiate, maintain, and escalate sexual behaviour with males (Beach, 1976; Fedigan, 1982). Such active attempts on the part of the females to solicit sexual interactions are defined as *female proceptive behaviours* (Beach, 1976).

Female Japanese macaques exhibit a variety of sexually proceptive stances, movements, gestures, and vocalizations, all which they employ when courting and in consortships with males (for detailed behavioural repertoires, see Enomoto, 1974; Leca et al., 2014b; Vasey, Chapais, & Gauthier, 1998). One sexual behaviour that is of particular interest is female-male mounting, which females routinely exhibit in some Japanese macaque populations (Gouzoules & Goy, 1983; Leca et al., 2014b; Wolfe, 1979a). According to Beach (1968, 1976), female-male mounting in mammals is proceptive because (a) it is clearly oriented towards the males, (b) the behaviour's frequency and intensity peak when females are in oestrus, and (c) it triggers and intensifies sexual excitement in males, encouraging them to mount.

In Japanese macaques, the first two points are supported by observational (e.g. Vasey, 2002a) and empirical (O'Neill et al., 2004a, 2004b) evidence, respectively. In line with Beach's latter point, Vasey (2002a, 2006, 2007; see also VanderLaan et al., 2012) has proposed that female-male mounting in this species is adaptive in nature, functioning

to prompt sexually sluggish or disinterested males to mount females in return. Some evidence exists to support this claim. In this primate species, female-male mounting occurs exclusively during sexual contexts (Dixson, 2012). Second, anecdotal evidence indicates that female-male mounts occur directly upon males' departure from consorting females' close vicinities (Vasey, 2002a). Third, female-male mounting occurs at an overall higher frequency when males exhibit low levels of female-directed mounting and solicitations (Leca et al., 2014b). Fourth, female-male mounting is more frequent in groups that contain higher proportions of senescent males, who mount and solicit females significantly less often than younger males (Leca et al., 2014b). While these findings lend themselves to the "disinterested male" portion of Vasey's hypothesis, the proposed mount-prompting function of this behaviour has not yet been tested in Japanese macaques, or any other species. To do so, the effect of female-male mounting on males' subsequent mounting behaviour, which is presumably related to mating success, must be investigated.

The adaptive, fitness-enhancing function of any behaviour is the reason *why* it has been selected for over evolutionary time and currently exists. To explain *how* this functionality is manifested, the proximate mechanisms, that is, the immediate triggers that generate its expression, need to be explored (Bateson & Laland, 2013; Scott-Phillips, Dickins, & West, 2011). Proximate triggers of sexual behaviours range from physiological ones (e.g. hormones), to social ones (e.g. the behaviour of conspecifics) to ones pertaining to the physical environment (e.g. temperature; Crews & Moore, 1986).

Some of the proximate mechanisms associated with female-male mounting in Japanese macaques have been investigated. Research indicates that females' pursuit of

immediate sexual reward likely serves as a proximate motivational influence on the occurrence of female-male mounting. In a study by Vasey and Duckworth (2008), two thirds of all female mounters exhibited genital stimulation during female-male mounts, which occurred via pelvic thrusting against the body of the male mountee, or via tail stimulation of the VPA region. Approximately half of all observed female-male mounts involved such stimulation.

A key feature of female-male mounting which makes it unique compared to other proceptive behaviours is that its successful execution requires the participation of two individuals: a mounter and a mountee. To fully understand the proximate mechanisms associated with this proceptive behaviour, an analysis of the *dyadic interactions* associated with mounting must be conducted. Specifically, what male behaviours, if any, prompt females to initiate female-male mounting? What female behaviours do males respond to when allowing themselves to be mounted? In Japanese macaques, females have been anecdotally observed chasing and mounting their male mates upon their departure from the female's vicinity (Vasey, 2002a). However, whether the male's departure is a proximate mechanism associated with female-male mounting has not yet been empirically validated. Further, additional behavioural triggers of female-male mounting (e.g., female grasping, female movement, male-female mounting) have yet to be examined.

Given the lack of knowledge regarding the ultimate function and proximate mechanisms associated with female-male mounting, I sought to examine both in this chapter. I began by providing general descriptive information regarding behavioural events and states observed before, during, and after female-male mounting. I then

examined the movements and actions involved in executing female-male mounts. To do

so, I provided qualitative descriptions of pre-mount movement sequences to determine

what male movements and actions (for definitions, see Methods) triggered females to

engage in the mounting process, and what female movements and actions prompted

males to position themselves to *be* mounted. Finally, I investigated the function of

female-male mounting by comparing male mounting activity after successful and non-

successful female-male mounts. If Beach's (1968, 1976) claim and Vasey's (2002a,

2006, 2007) Japanese macaque-specific hypothesis holds true, the likelihood that and the

rate at which male-female mounting occurs following female-male mounting should be

higher compared to instances in which a female-male mount was attempted but did not

successfully occur.

Methods

Subjects and Study Site

The Japanese macaques observed in this study were members of the Arashiyama-

E troop, a free-ranging and provisioned group of monkeys residing in and around the

Iwatayama Monkey Park, located in the suburb of Arashiyama, in the northwestern

outskirts of Kyoto city, Japan (Huffman et al., 2012). Sexually mature individuals were

exclusively selected for analyses; specifically, females aged 5 years or more (Leca et al.,

2014a) and males aged 4 years or more (Hanby & Brown, 1974). These macaques were

observed and recorded during the fall-winter mating seasons of 2001-2002 (19 males and

91 females), 2003-2004 (17 males and 95 females), 2010-2011(11 males and 93 females),

and 2011-2012 (10 males and 97 females), each with a socionomic sex ratio (proportion

of sexually mature males to sexually mature females) of 1:4.8, 1:5.6, 1:8.5, and 1:9.7,

respectively. The ratio of individuals per age and sex classes and the matrilineal composition of the troop were considered to be typical for free-ranging groups of this species (Yamagiwa & Hill, 1998).

Data Collection

Observational protocols. The focal animal sampling method (Altmann, 1974) was employed when video-recording all female-male and female-female mounting. For the 2001 and 2003 field seasons, consortships were recorded in 30-minute time blocks, unless (1) the observer lost sight of the dyad, (2) the consortship lasted less than 30 minutes, or (3) another consortship for which less data had been collected was observed (Vasey & Duckworth, 2006). For the 2010 and 2011 field seasons, consortships were recorded in two consecutive 30-minute time blocks, with day-by-day selection of focal samples determined by a list prepared in advance (Leca et al., 2014a).

Partner-wise notation. Video sequences of behaviour directly before, during, and after female-male mounting were analysed using the principles of partner-wise EWMN, a globographic reference system that qualitatively describes the spatial and temporal relationships between individuals in a variety of contexts (Eshkol & Wachman, 1958; see also Pellis, Blundell, Bell, Pellis, Krakauer, & Patricelli, 2013 (agonistic interactions); Reinhart, Pellis, Thierry, Gauthier, VanderLann, Vasey, & Pellis, 2010 (play fighting). To the best of my knowledge, this is the first study to use partner-wise EWMN to quantify primate consortship behaviour. Specifically, individuals' relative *positions*, *movements* and *actions* were scored.

The *relative position* of consorting individuals included their *relative horizontal distance* and their *relative body orientation*. The *relative horizontal distance* between the

two consorting partners had three possible values: touching, an arm's length apart, or greater than an arm's length apart. *Relative body orientation* was defined in terms of the sitting consort partners' body planes that most closely opposed each other, with body planes being divided into chest (front), back, and side. Relative body orientation was also noted when individuals were in a non-sitting position, but these were infrequent. These variables were scored: (1) immediately before the occurrence of any body movement leading to a female-male mount, when both individuals were still, and (2) immediately after a female-male mount, when the female dismounted and both individuals had settled into a sitting position. Pre- and post-mount *stance* (i.e. sitting or standing) was also scored for both individuals.

A mount-related *movement* was defined as a change in the position of any below-neck body segment that directly contributed to carrying out a successful or failed mount attempt. This included the female turning her torso to readjust her position relative to the male, the female leaning her torso forward or to the side (to get up, or push herself against the male), the female lifting her arms to grasp the male, and the male leaning his torso forward to get up. Head movements were excluded from sequence analyses as they occurred frequently throughout consortships and were not essential in executing female-male mounting. A mount-related *action* occurred when an individual's hands were touching or grasping another individual's hindquarters. This included the female grasping or laying her hands upon the male's hindquarters, the male placing his hands on the female's hindquarters, and the male grasping the female's hindquarters while mounting or dismounting the female.

I also scored the *relative order* of the movements and actions that occurred during a female-male mounting sequence. A mounting sequence began at the frame in which the female or male performed the first below-neck movement or action which directly contributed to carrying out a mount. The movement or action that initiated a female-male mount sequence was clearly identifiable, as directly prior to the sequence, individuals held stable positions.

Other behavioural measures. A mounting sequence could result in either a successful or failed mount. A female-male mount was *successful* (i.e. completed) when the female placed herself upon the male and clasped her feet anywhere along his legs (for operational definitions of each mount type, see Chapter 3). A *failed* mount occurred when the female attempted to mount by forcibly pushing her body against the male and/or grabbing the male's hindquarters, but did not place herself upon the male via foot-clasping.

Inter-mount intervals were calculated by subtracting the time at which a female-male mount ended from the time at which the next female-male mount occurred, or in some cases, when the subsequent male-female mount resulting in ejaculation occurred. An inter-mount interval began when two of the female's limb extremities (hands and/or feet) touched the ground upon dismounting. An inter-mount interval ended at the frame in which the female (or male, in cases of ejaculatory mounts) performed her (or his) first below-neck movement directly contributing to carrying out a mount.

Within inter-mount intervals, the occurrence of each male-female mount was recorded. The rate of male-female mounting was calculated by dividing the number of male-female mounts by the duration of the inter-mount interval. Any occurrence of male-

to-female solicitation behaviour (i.e. intense eye gazing, lip smacking, etc.; see Leca et al., 2014b) immediately before (i.e. within 3 seconds) a female-male mount was scored. During female-male mounts, the horizontal distance traveled by the male (and consequently, the female) (i.e. ≤ 1 monkey length) and the occurrence of male arousal-related sexual behaviours, including sexual solicitations (i.e. gazing back, grasping of the female) and self-directed sexual behaviour (i.e. masturbation) was also scored.

Data Analysis

Ten female-male mounts were selected from 10 unique consortships ($N = 100$ female-male mounts), with each dyad being composed of one unique male and female. To further increase the comparability of mounts between consortships, the first 10 female-male mounts that occurred within the same day were selected from each consortship.

As the movements and actions performed during female-male mounting sequences often occurred in rapid succession, frame-by-frame analysis (1 frame = .033 s) was used to determine when they occurred, which of the two partners was performing them, and the order in which they occurred.

Because the data pertaining to relative orientation and movement were nominal, and scale data were not normally distributed, non-parametric statistics were used for all analyses (Siegel & Castellan, 1988). Chi-square tests of independence and goodness-of-fit tests were used to analyse nominal data, and Mann-Whitney U tests were used to analyse scale data.

<div align="center">**Results**</div>

General Descriptive Pre- and Post- Female-Male Mounting

      Partner-wise orientation. The relative horizontal distance and body orientation observed between consort partners directly prior to a female-male mount ($N = 100$) are displayed in Table 2.1 and Table 2.2, respectively. The relative horizontal and body orientation observed between consort partners after successful female-male mounts ($N = 69$) are shown in Table 2.3 and Table 2.4, respectively.

      Non-mounting male behaviour. Prior to female-male mounts ($N = 100$), 30.0% of males ($N = 4$ mounts) were observed soliciting the female mounter. During successful female-male mounts ($N = 70$ mounts), 30.0% of males ($N = 13$ mounts) were observed exhibiting at least one form of arousal-related sexual behaviour during at least one female-male mount ($N = 7$ masturbating, $N = 8$ gazing back, $N = 2$ grasping). Also, 88.6% of successful mounts involved the males remaining stationary (≤ 1 monkey length travelled) as they were being mounted.

Proximate Mechanisms: Partner-wise Movements and Actions

      Seven female-male mounting sequences involving male and female movements and actions were first distinguished, and later grouped into female- or male-initiated sequences. These categories of sequences are as follows:

Female-initiated mounting sequences

Category #1. Attempted female-male mount → unresponsive male: The *female attempts* to mount the male (i.e. grasping his hindquarters area, pushing her body against his side or back); the *male does not get up* and/or responds with aggression. No female-male mounting occured.

Category #2. Female movement to mount→ female grasp → male movement to be mounted: The *female moves* to mount the male (i.e. shifts arm position, turns torso, leans forward to get up); the *female grasps*/lays her hands on the male's hindquarters area; the *male moves* to stand up (i.e. leans torso forward). Successful female-male mounting occurred in 90.0% of the cases in this category.

Category #3. Female movement to mount → male movement to be mounted→ female grasp: The *female moves* to adjust herself into the mounting position (i.e. shifts arm position, turns torso, leans forward to get up); the *male moves* to stand up (i.e. leans torso forward); the *female grasps* the male's hindquarters area with her hands. Successful female-male mounting occurred in 84.6% of the cases in this category.

Male-initiated mounting sequences

Category #4. Male movement → female movement to mount→ female grasp: The *male moves* (i.e. shifts arm position, turns torso, leans); the *female moves* to mount the male (i.e. shifts arm position, turns torso, leans to get up); the *female grasps* the male's hindquarters area. This always resulted in successful female-male mounting.

Category #5. Male departure → female movement toward the male → female grasp: The *male stands* and *departs* (i.e. walks away, runs away) from his original stationary position (which is in close vicinity of the female); the *female* catches up with the male, and *grasps* the male's hindquarters area. This always resulted in successful female-male mounting.

Category #6. Male-female mounting → female-male mounting: The *male* is either in the process of *mounting, dismounting*, or *mount prompting* (i.e. hand-on-hindquarters); the *female moves* to mount the male (i.e. reaches back, turns torso) and *grasps* the male's hindquarters area. This always resulted in successful female-male mounting.

Other

Category #7. Ambiguous sequence of events: The order of movements and actions within

the mounting sequence is ambiguous. This is either due to the sequence-initiating

movements or actions being performed by both individuals in the same frame, or the

male's initial movement in response to the female's movement not being conducive to

being mounted. This always resulted in successful female-male mounting.

Given that the departure of males has been anecdotally mentioned as a cause for

female-male mounting (Vasey, 2002a), case-by-case detailed descriptions of the events

surrounding female-male mounts in Category #4 and #5 were conducted (see Appendix).

The observed frequencies for each category are displayed in Table 2.5. Frequencies

across all seven sequence categories differed from one another (χ^2[6, N = 100] = 56.52 , p

< .001). When split into initiator-based groups, female-initiated categories (79.0 %) were

significantly more frequent than male-initiated mounts (18.0 %; χ^2[1, N = 97] = 38.36 , p

< .001). Female-initiated categories also appeared to be the most commonly observed

across consortships (Category #1 = 60% of consortships, Category #2 = 80%, Category

#3 = 80%), while male-initiated mounts appeared to be less common overall (Category

#4 = 30%, Category #5 = 40%, Category #6 = 40%).There was no significant difference

in frequency across the three female-initiated categories (χ^2[2, N = 79] = .58, p = .747), or

across the three male-initiated categories (χ^2[2, N = 18], = .23, p = .322).

Ultimate Function: Male Mounting Following Female-Male Mounting

The effect of female-male mounting on subsequent male-female mounting was

tested by comparing *failed* female-male mounts (N = 30), composed of all attempted

female-male mounts from Category #1 and failed female-male mounts from Category #2 and #3, to *successful* female-male mounts composed of all remaining mounts ($N = 70$).

The occurrence of a female-male mount increased the likelihood of subsequent male-female mounting to occur (χ^2 [1, $N = 100$] = 10.49, $p < .001$), with male-female mounting being more likely to occur after a successful female-male mount, and less likely to occur after a failed female-male mount attempt.

The rate of male-female mounting was significantly higher following a successful female-male mount than following a failed female-male mount (Mann-Whitney U test = 1448, $p = .001$). The average frequency of male-female mounting was .55 per minute (SD = .664) following a successful female-male mount, and .15 mounts per minute (SD = .446) following a failed female-male mount. This result was not affected by differences in inter-mount interval duration between successful and failed mounts ($U = 1038$, $p = .928$).

Discussion

Female-male mounting is a significant facet of the female sexual behaviour in some populations of Japanese macaques (Leca et al., 2014b). This non-conceptive sexual behaviour has been described previously in this species (e.g. Wolfe, 1979a; Gouzoules & Goy, 1983). However, the proximate mechanisms that underlie and influence female-male mounting had been relatively unexplored (for a notable exception, see Vasey & Duckworth, 2008). Also, the adaptive nature of female-male mounting, with respect to mating success, had yet to be empirically tested. In the current study, the proximate mechanisms underlying female-male mounting, as well as the adaptive utility of this behaviour, were investigated.

The Proximate Mechanisms of Female-Male Mounting Sequences

In this study, I aimed to examine how the movements and actions of both male and female consort partners incited males to stand and be mounted by their female consort partners, and triggered females to mount males. A total of seven distinct female-male mounting sequences were identified, each falling into one of the following two groups: (1) those initiated by female movements (Categories #1, #2 and #3), and (2) those initiated by male movements (Categories #4, #5 and #6).

Female-initiated sequences were the most frequent, making up 79% of all mounts and expressed in the majority of dyads (i.e. Category #1: 60%; #2: 80%; #3: 80%), suggesting that, instead of responding to male behaviour (Vasey, 2002a), female-male mounting is largely driven by internal motivation on the part of the female. Female mounting motivation in Japanese macaques is likely influenced by a variety of individual factors, such as oestrus level (O'Neill et al., 2004a), age, presence of other competing females (VanderLaan et al., 2012), the frequency of male sexual solicitations during consortships (Leca et al., 2014b), and the types of solicitations males display (this study). To gain a comprehensive understanding of the proximate mechanisms influencing female-male mounting in Japanese macaques, future research needs to take into account the relative contribution of each of these factors.

The manner in which males responded to females' actions and movements before and during female-initiated mount sequences is particularly noteworthy. In one third of female-initiated mounts, males began moving to stand moments *after* females grasped their hindquarters. This hands-on-hindquarters solicitation is a tactile form of courtship employed by Japanese macaques as a request to mount their consort partners (Vasey et

al., 1998). While it is commonly used to prompt the mounting of females within homosexual (Vasey et al., 1998) and heterosexual consortships (Enomoto, 1974), data presented in this chapter indicate that females also use this courtship behaviour to prompt males to be mounted. Therefore, the hands-on-hindquarters manoeuver can be considered a *signal*, that is, a behaviour that has evolved to communicate a specific message and change the behaviour of the signal receiver in a manner that is adaptive to one or both individuals (see Karlson & Luscher, 1959; Marlk, 1983). As a signal, the hands-on hindquarters solicitation would be used by females to communicate their desire to mount males. Given that Category #1 mounts also involved females performing hand-on-hindquarters prior to any male movements, but with males being unresponsive, the signal succeeded in affecting the male's behaviour about half of the time.

Also, one third of female-initiated mounts involved males that positioned themselves to be mounted *before* their female partners grasped them. In such cases, males began to stand to be mounted directly after the female reoriented herself in preparation for a mount. Therefore, in addition to explicit sexual solicitations, female movements that are produced as *by-products* of the imminent female-male mount attempts also trigger males to stand to be mounted. Thus, it appears as if males interpret these movements as *cues* of imminent female-male mounting, in other words, movements that carry useful information *incidentally*, but have not been naturally selected for communication purposes (see Seeley, 1995). By reacting to such incidental movements, it could be argued that males anticipate and facilitate female-male mounting. Additionally, given that Category #1 mounts also involved females exhibiting mounting cues prior to male movement, but with males being unresponsive, female-male mounting cues succeeded in

affecting the male's behaviour about half of the time. Research pertaining to feeding

ecology also illustrates how cues can be interpreted in an adaptive manner with respect to

foraging choices. The quality of a food source, for example, can be assessed by observing

the incidental behavioural cues of other individuals attempting to exploit it. While the

foragers' behaviour is informative to others, it did not evolve to publicly communicate

resource quality, and does so only incidentally (Schaefer & Ruxton, 2012). In terms of

primate sexuality, skin redness in females is caused by increased blood flow

vascularization, which is a direct result of estrogen surges during oestrus (Dixson, 2012).

Males are known to respond sexually to such redness in sexual contexts (e.g. Bielert,

Girolami, Jowell, 1989; Waitt, Gerald, Little, & Kraiselburd, 2006). However, it is

unclear whether redness was naturally selected to *signal* fertility, or if it is simply a by-

product of females' hormonal state, and hence a fertility *cue* (Jones et al., 2015).

Overall, it is clear that males are prompted to assume the mountee position when

exposed to both explicit sexual solicitations and incidental movements performed by their

female consort partners. But why do males allow females to mount them in the first

place? Beach (1976) has hypothesized that female-male mounting sexually excites males.

Given that female-male mounting is considered to be a proceptive behaviour (Beach,

1976; Dixson, 2012; O'Neill et al., 2004a), it may have evolved as an inherently

attractive and solicitous action to males, sexually exciting them (presumably) in the same

manner as other proceptive behaviours do, such as head-bobbing or ground smacking. It

can also be speculated that the anticipation of proximate sexual reward received by males

when mounted by females plays a role in the male compliance. In the Arashiyama-E

population of Japanese macaques, the vast majority of female-male mounts are double

foot-clasp and reclining mounts (Vasey & Duckworth, 2008). Apart from the possibility

of brief genital contact occurring as the female climbs and positions herself upon the

male, reclining mounts generally do not result in the male's genitals coming into contact

with the female's body. In contrast, double foot-clasp mounts – which involve the female

positioning herself directly behind the male's rump – may afford the male some genital

stimulation, particularly in cases where female thrusting is involved. In the current study,

males were observed masturbating, gazing back at, or grasping the female in 19% of

female-male mounts, further implying that males may obtain some sort of sexual

stimulation while being mounted and thrusted against by females.

If female-male mounting is indeed sexually gratifying to males, their level of

sexual arousal may be deduced by the type of stimuli to which they react during female-

initiated mounting sequences. For example, unresponsive males (Category #1 mounts)

could be considered to display little to no sexual arousal. In contrast, female-male mounts

prompted by hands-on-hindquarters performed by females indicates substantial male

sexual arousal, given that the males are willing to position themselves to be mounted

following prompting. Moreover, female-male mounts prompted by incidental female

movement are suggestive of heightened male sexual arousal, given that such males

appear to anticipate and facilitate mounts independent of any explicit prompting.

Female-male mounts initiated by male movements (Categories #4 and #5) were

significantly less common than those initiated by female movements. Their occurrence

did, however, corroborate previous anecdotal reports. Specifically, the sequences in

which a female mounted a male upon the male's departure from his original position are

in line with what has been anecdotally described in the literature (Vasey, 2002a).

According to Vasey (2002a, 2006, 2007), this particular mounting sequence is consistent with the view that female-male mounting in such circumstances may function to focus the departing male's attention on the consortship. By the same token, females also appeared to be sensitive to male movements on a much smaller scale, as they sometimes initiated grasping actions directly following males' attempts to stand or reposition themselves. If females sometimes mount males to maintain attention and spatial proximity during consortships, then it is possible that females interpret small movements by males as indications of their partners' imminent departure from their vicinity and mount them in anticipation of this event. To test the proposed attention/proximity function of female-male mounting in Japanese macaques, future studies must focus on female-male mounts initiated by the male's departure and movements, and observe the male's behaviour after such mounts.

Females also occasionally performed a female-male mount as they were being mounted, dismounted, or sexually solicited by males via hands-on-hindquarters. In such cases, it is possible that the intromission or solicitations increased the females' sexual arousal and, in turn, prompted them to seek further immediate sexual reward via genital stimulation during a female-male mount.

Lastly, ambiguous mounts occurred when the order in which initiating movements, and subsequent movements and actions leading to the female-male mount were not clear. Despite there being no clear initiator, such sequences always resulted in successful female-male mounts, suggesting that both males and females are motivated to engage in female-male mounting.

The Function of Female-Male Mounting

Female-male mounting is considered to be a sexually proceptive behaviour (Beach, 1968, 1976), hypothesized to gain the attention of male consort partners and enticing them to mount in return (Vasey, 2002a, 2006, 2007). In the Arashiyama population of Japanese macaques, females mount males frequently, sometimes upon their departure from the females' vicinity, and males have been anecdotally observed mounting females shortly after (Vasey, 2002a). Consequently, it has been suggested that female-male mounting in Japanese macaques is adaptive, functioning to prompt males to mount females in return (Vasey, 2002a, 2006, 2007).

In this study, the functional aspect of female-male mounting was tested by examining its effects on subsequent male mounting. Specifically, compared to instances in which female-male mount prompting occurred but was *not* followed by female-male mounting, successful female-male mounting (a) *increased* the likelihood of subsequent male-female mounting occurring, and (b) resulted in an overall *greater* rate of male-female mounting (i.e. more male-female mounts were performed during the period following female-male mounting and until the last male-female mount leading to ejaculation). Together, these results support the view that female-male mounting functions to eliciting male-female mounting. For a behaviour or trait to be ultimately adaptive, however, it must increase an individual's fitness in some way. While it is likely that female-male mounting increases chances of conception by prompting male mounts, the behaviour's correspondence with other reproduction-related outcomes, such as male ejaculation (via intromission) and subsequent pregnancy, must also be investigated in future research.

Table 2.1. *Relative horizontal distance between consortship partners before female-male mounting*

Distance	Percentage
Touching	69.0
Arm's length	19.0
> Arm's length	12.0

N = 100

Table 2.2. *Relative body orientation before female-male mounting*

Female-to-Male Orientation	Percentage
Chest to back	24.2
Back to chest	14.1
Side to side	13.1
Side to back	11.1
Back to back	9.1
Back to side	8.1
Mounted to mounting[a]	7.1
Chest to side	6.1
Side to chest	2.0
Chest to chest	1.0
Other (one individual in a non-sitting position)	4.1

N = 99

Note. Final *N* is due to one mounting sequence involving a male that was out of frame.

[a]Mounted to mounting orientation refers to the cases in which the male was mounting the female directly prior to the female initiating female-male mounting

Table 2.3. *Relative Horizontal Distance Between Consortship Partners After Female-Male Mounting*

Distance	Frequency	Percentage
Touching	40	58.0
Arm's length	24	34.8
> Arm's length	5	7.2

N = 69

Table 2.4. *Relative Body Orientation After Female-Male Mounting*

Female-to-Male Orientation	Percentage
Back to chest	42.0
Chest to back	15.9
Back to side	15.9
Side to side	13.0
Side to chest	5.8
Back to back	4.4
Chest to side	1.5
Side to back	1.5

$N = 69$

Table 2.5. *Percentage of Observed Female-Male Mounts across Sequence Categories*

Sequence Category	Percentage
1	23.0
2	30.0
3	26.0
4	5.0
5	4.0
6	9.0
7	3.0

$N = 100$

CHAPTER THREE

A Structural Comparison of Female-Male and Female-Female Mounting: The Nature of their Evolutionary Link

Abstract

Japanese macaques are unique in their sexual behaviour, as adult females, in some populations, perform two forms of non-conceptive mounting: female-female and female-male. According to Vasey's model, both forms of mounting are closely phylogenetically related, with female-female mounting hypothesized to be the functionless by-product of the adaptive female-male mounting. While evidence exists to support both these claims separately, a structural comparison is needed to further understand the phylogenetic link between these two forms of mounting. In this study, the phylogenetic relatedness between these two forms of mounting was further investigated by comparing the body segment positions employed by female mounters during homosexual and heterosexual mounts. None of the eight segments measured differed between female-male and female-female mounters, thus supporting the notion that both forms of mounting are evolutionarily linked. While this result supports Vasey's proposed model, the complete lack of differences between both mount forms was peculiar, as factors such as differences in mountee body size and different selectional forces operating on the two could affect their structural expression.

Introduction

Evolutionary inquiries about behaviour, which address *why* a behaviour exists in its current form, come in two varieties. *Functional* questions examine the behaviour's fitness-enhancing (i.e. adaptive) utility. This involves examining potential ways in which a behaviour contributes toward an organism's survival and reproduction in a positive manner (Tinbergen, 1963; Vasey, 2007). *Phylogenetic* questions examine the behaviour's evolutionary history from its point of origin to its current form. This involves examining the step-by-step manner in which a behaviour originated and changed over time (Tinbergen, 1963; Vasey, 2007). For example, Dixson (2012) proposed an evolutionary scenario describing the emergence of different types of mounting in primates. He posits that the ventro-ventral copulatory mount is derived from dorso-ventral mounting, as the latter is widespread amongst primates, while the former is largely restricted to the great apes. While the majority of evolutionary research tends to focus on questions pertaining to the adaptive value of traits, both questions are complementary, and arguably, equally important in understanding the evolution of a behaviour (Vasey, 2007).

Both of these ultimate approaches to behaviour have been invoked to understand non-conceptive mounting in female Japanese macaques, which manifests prominently in two distinct forms: female-male and female-female mounting (Gouzoules & Goy, 1983; Leca et al., 2014b; Wolfe, 1979a). An adaptive value for female-male mounting—a proceptive behaviour that occurs exclusively during heterosexual consortships (Dixson, 2012, O'Neill et al., 2004a) —has been proposed. Specifically, female-male mounting in Japanese macaques is hypothesized to sexually excite males, prompting them to mount females in return and focus their attention on the consortship at hand (Vasey, 2002a,

44

2006, 2007). Three lines of evidence are consistent with this hypothesis. First, intergroup comparative data have shown that female-male mounting is more frequent in groups where most resident males are old and sexually under-motivated (Leca et al., 2014b). Second, behavioural evidence indicates that female-male mounting increases subsequent male-female mounting, thereby presumably increasing the chances of conception (Chapter 2). Third, hormonal evidence has shown that the rate of female-male mounting is higher during the follicular and periovulatory phases of the ovarian cycle than during the luteal phase (O'Neill et al., 2004a, 2004b).

The possible functional aspects of female-female mounting, which occur exclusively within homosexual consortships, have also been investigated (Vasey, 2006, 2007; Wolfe, 1986). However, despite numerous empirical tests, female-female mounting has not been found to facilitate ulterior social goals, such as communicating dominance rank (Vasey et al., 1998), encouraging alliance formation (Vasey, 1998), or post-conflict resolution (Vasey, 2004b), to name a few (reviewed in Vasey, 2002a, 2002b; Vasey & VanderLaan, 2012). While female-female mounting does not appear to be an adaptation, this behaviour is sexual in nature, with several lines of evidence support this conclusion. First, it occurs exclusively within homosexual consortships which closely resemble heterosexual consortships (Vasey, 2002a). Second, female-female mounting does not occur between close kin (Chapais et al., 1997; Gunst et al., 2015). Third, female-female mounting is largely driven by proximate sexual reward, which females obtain by stimulating their vulvar/perineal/anal (VPA) region during mounts (Vasey & Duckworth, 2006). Fourth, like female-male mounting, female-female mounts are more frequent during the follicular and periovulatory phases than during the luteal phase, indicating that

45

both heterosexual and homosexual female mounts are influenced by similar hormonal mechanisms (O'Neill et al., 2004a, 2004b).

So, why does female-female mounting occur so frequently if it does not serve any adaptive purpose? In addition to adaptations, the evolutionary process also produces characteristics that exist and persist due to them being incidentally coupled with adaptations, otherwise known as *by-products* of adaptations (Buss et al., 1998). Consequently, by-products of adaptations do not have an evolved fitness-enhancing function (Buss et al., 1998). It has been proposed that female-female mounting in Japanese macaques is a by-product of female-male mounting (VanderLaan et al., 2012; Vasey, 2002a, 2006, 2007), as it does not appear to have any adaptive value, and shares some striking similarities with a supposedly adaptive co-occurring behaviour (i.e. female-male mounting).

To explain the ultimate reason for the existence of female-female mounting, and consequently, the evolution of non-conceptive mounting behaviour in female Japanese macaques as a whole, the historical/phylogenetic approach must be invoked. Vasey (2002a, 2007; see also VanderLaan et al., 2012) has proposed a step-by-step trajectory for female mounting, with each hypothesized evolutionary step being supported by some evidence. The model incorporates evidence based on current data on mounting among juvenile males and adolescent females, as well as female-male, male-female, and female-female mounting among adults in this species.

The model begins by noting that male-male mounting and mount attempts are commonly observed between juvenile males of this species (Gunst et al., 2013; Hanby, 1974). Evidence indicates that play mounting among immature male Japanese macaques

functions to solicit the attention of play partners (VanderLaan et al., 2012). Therefore, non-conceptive mounting may have originated as an element of male-specific social play, as juvenile males respond to being mounted by focusing their attention on the mounter. Second, at some point in the species' evolutionary history, females' ability to perform female-male mounting was selected for because it functioned as a proceptive behaviour that focused the male's attention on the mounting female and increased the male's sexual response by prompting him to partake in potentially conceptive male-female mounting (Chapter 2). Third, females evolved the ability to obtain immediate sexual gratification when mounting males by rubbing their VPA regions onto the back of their male partners or with their own tails (Vasey & Duckworth, 2008). Fourth, over evolutionary time, female-female mounting emerged as a by-product of the adaptive female-male mounting, with proximate sexual reward being its primary underlying causal mechanism (Vasey & Duckworth, 2006). Given that heterosexual interactions are more likely to result in male-induced injury to females than homosexual ones, female-female mounting appears to be safer than male-female mounting when it comes to obtaining sexual reward (Leca et al., 2014d). Consequently, small-bodied and vulnerable adolescent female Japanese macaques may routinely engage in homosexual interactions to avoid aggression from adult males (Gunst, Leca, & Vasey, 2015).

The idea that female-female mounting is a by-product of female-male mounting is consistent with the manner in which these two forms of mounting co-occur across different Japanese macaque populations. Indeed, Leca et al. (2014b) found that female-male mounting either existed on its own in some groups or in conjunction with female-female mounting. In contrast, female-female mounting only occurred in groups where

female-male mounting was present. This result is consistent with Vasey's proposed evolutionary scenario, which holds that female-male mounting is the predecessor of female-female mounting, and the latter should not exist without the former being present.

In this chapter, I aim to further expand upon the proposed phylogenetic link between female-male and female-female mounting by comparing the structural characteristics that define both forms of mounting. Mount structure, as defined by the limb positions employed by heterosexual and homosexual female mounters, will be measured by using the Eschkol-Wachman Movement Notation, a globographic referencing system which quantifies individual's body segment positions in space (Eshkol & Wachman, 1958). A lack of differences in the positions employed between the two forms of mount would provide further support to the proposed phylogenetic link between the two. While the occurrence of differences would not provide support for the hypothesis, it would not necessary provide evidence *against* it either. Instead, small differences between the two forms of mounting might reflect disparity in body size ratio between partners in homosexual versus heterosexual consortships, or a discrepancy in the motivations underlying female-female mounts (which are explicitly driven by self-directed sexual reward) versus female-male mounts (which may have specific proceptive properties). Differences may also indicate that selection is constraining the expression of female-male mounting—a purportedly adaptive behaviour—whereas, female-female mounting, which lacks fitness consequences, is not under such strong stabilizing selection.

<p style="text-align: center;">**Methods**</p>

Subjects and Study Site

The subjects and study site were identical to those described in Chapter 2.

Data Collection

Observational protocols. The observational protocols were identical to those described in Chapter 2.

EWMN. A total of eight body segments were analyzed: lower torso, mid-torso, upper torso, upper arm, lower arm, upper leg, lower leg, and foot. Their physical positions in space were quantified using the Eshkol-Wachman Movement Notation (EWMN), a globographic reference system which describes the three-dimensional movements of body segments (Eshkol & Wachman, 1958). In this study, however, EWMN was used to measure the position of unmoving body segments only. As described by Whishaw and Pellis (1990), EWMN views the body as a system composed of connected axes (body segments), which either lie between two rotation points (joints) or are double-ended by a joint and a free extremity. Segment positions are measured by placing the central point of the reference sphere (hereby referred to as the reference point) on the weight-bearing joint of the segment, with the segment imagined as being a straight line (Whishaw & Pellis, 1990). The EWMN unit which the line lies the closest to is deemed to be the position of the segment in question. The standard EWMN sphere is divided into eight separate 45° units in the horizontal and vertical planes (Figure 3.1). For more fine-grained analyses, segment positions in this study were measured to the nearest half-unit (i.e., 22.5°), resulting in a total of 16 EWMN units that could potentially be observed (Figure 3.2).

<p style="text-align: center;">49</p>

Body segments. Each of the eight body segments fell into one of two categories; the spine and the distal limbs. The location of all body segments are shown in Figure 3.3.

The *spine* contains three distinguishable segments, and comprises two points of flexion and/or extension: (a) the lumbosacral junction (vertebrae S1 to L7, approximately) between the lower and mid-torso, and (b) the thoracolumbar junction (vertebrae L1 to T12, approximately) between the mid- and upper torso. In order to approximate the location of spinal segments and joints, I applied human anatomical information, obtained from Gray (1918) and Palastanga and Soames (2012), to the Japanese macaque spine as described by Tasumi (1969). The spine segments were characterized as follows:

(1) Lower torso (also known as the pelvic area): Spine segment located between the base of the tail and the posterior end of the lumbar spine. The reference point was set at the base of the tail.

(2) Mid-torso (also known as the lumbar region of the spine): Spine segment located between the posterior end of the lumbar region and the posterior end of the thoracic region. The reference point was set at the lumbosacral junction.

(3) Upper torso (also known as the thoracic region of the spine): Spine segment located between the anterior region of the lumbar spine and the base of the neck. The reference point was set at the thoracolumbar junction.

The *distal segments* were characterized as follows:

(1) Upper arm: Limb segment located between the posterior side of the elbow and the posterior side of the shoulder. Unlike the other distal limb segments, the upper arm's position was measured straight along the posterior length of the limb, as in many cases,

50

the long fur on the animals' upper arm and chest obstructed the anterior side of the upper arm. The reference point was set at the elbow joint.

(2) Lower arm: Limb segment located between the center of the wrist region and the center of the elbow region. The reference point was set at the wrist joint.

 (3) Upper leg: Limb segment located between the center of the knee region and the center of the upper thigh region. The reference point was set at the knee joint.

(4) Lower leg: Limb segment located between the center of the ankle region and the center of the knee region. The reference point was set at the ankle joint.

(5) Foot: Limb segment located between the bottom of the heel and the edge of the small toe. The foot's position was measured straight along the medial length of the limb, as in many cases, the long fur around the animals' ankle obstructed the lateral side of the foot. The reference point was set at the start of the small toe.

Mount types. Adapted and modified from previously established definitions (Vasey, 2002a; Vasey et al., 1998, 2006; Vasey & Duckworth, 2006), a *double foot-clasp mount* was characterized by both of the mounter's feet grasping the mountee's lower leg anywhere between and including the ankle and the knee, coupled with their hands grasping the mountee along their hips or lower back. Two other types of mounts were also commonly performed by female Japanese macaques: *sitting mounts*, which occurred when the mounter was sitting in a jockey-like position on the mountee's back and grasping between the mountee's lower back with her hands, and their thighs and lower back with her feet, and *reclining mounts*, characterized by the mounter lying ventrally on the mountee's back with her feet grasping between the mountee's ankles and thighs and her hands grasping their upper back (Vasey, 2002a; Vasey et al., 2006; Vasey &

51

Duckworth, 2006). However, group comparisons were not possible for these two mount types due to the incomparable small sample sizes of homosexual and heterosexual mounts. Additionally, in order to be distinguishable from a reclining mount, double foot-clasp mounts that adhered to the mount type's definition but involved the mounter's lower chest coming into contact with the mountee's back were excluded.

Data Analysis

Using the Sony Vegas Pro video-editing program, observer-controlled frame-by-frame video seeking was used to determine the length of time mounts were stable and to obtain all images of mounts for EWMN (1 frame = .033 s). Also, given that mounts were captured using one camera and thus from only one angle, positions could only be accurately quantified in one plane. Therefore, vertical segment positions were measured, as all body segments were the most visible in this plane.

A mount was deemed usable for scoring by meeting the following criteria: (a) positioned in a profile-like manner (i.e. facing approximately 90° away from the camera, based on observer judgment), (b) approximately eye-level in view, (c) the mountee standing in the standard position (i.e. torso parallel to the ground, with upper and lower back legs both in the EWMN 4 position (approximately 90° perpendicular to the ground)), and (d) a minimum of .20 seconds in duration (6 frames).

In order to ensure that images were taken during a stable part of a mount, all mounting images were taken at the midpoint of their respective stability duration. Mount stability was defined by each of the mounter's eight body segments remaining in one EWMN position. A mount's stability began during the first frame in which all body segments held one EWMN position, and ended in the frame directly preceding the first

limb angle change leading to a perceived EWMN unit change of one or more body segments. Stability duration was calculated by subtracting the stability start time from the stability end time.

Upon capturing the image, the default direction in which monkeys were made to face was to the right. In cases that the captured mount was with left-facing monkeys, the image was flipped horizontally. It is also important to note that only the camera-facing side of the monkeys was quantified, with the other side being disregarded in both EWMN and mount stability duration.

Statistical analyses. As the EWMN positional data was ordinal in nature, non-parametric testing was used to conduct comparisons (Siegel & Castellan, 1988). Exact statistical methods were used to lessen the potential effect of a small sample size ($N = 26$) on the results (Mundry & Fischer, 1998). All statistical tests were two-tailed.

Two measures were taken to limit the potential effects of individual mounters on the results. First, six of the female mounters were found to partake in both forms of mounting, hereby referred to as the *heterosexual group* and *homosexual group*. Therefore, each was assigned to one of the two groups, with four designated to the heterosexual group and two designated to the homosexual group, resulting in a total of 13 individuals in each group. Since, compared to the homosexual group, a larger portion of the heterosexual group was composed of individuals mounting only once, dual-group females with more than one heterosexual mount were given precedence to being assigned to the heterosexual group. Second, mounters in both groups were unequally represented within the data set, with some being scored once, while others appeared as many as 22 times (Table 3.1). To mitigate the potential effects of this unequal representation of

mounters, statistical tests were run using one mount per individual. Within each individual mounter's pool of mounts, mounts were assigned numbers and selected for each round of testing by using a random number generator. To maximize the representativeness of any potential intra-mounter variability in limb positioning, statistical tests were repeated 30 times using this random selection methods. For each round of testing, scores for each mounter's body segments came from the same mount. To correct for multiple testing, the Bonferroni correction was implemented, resulting in a critical p value of .0017. Data were analysed using IBM SPSS 21.

One observer (L.O.C.) scored the entire data set Intra-rater reliability was assessed by re-scoring 30 randomly selected mounts. Cohen's kappa was used to determine the relatedness between these scores. As per the benchmarks set by Landis and Koch (1977), almost "perfect" agreement was reached for the mid-torso ($K = .832$, $p <$ .001), lower arm ($K = .829$, $p < .001$), and upper leg ($K = .881$, $p < .001$) scores, and "substantial" agreement was obtained for lower torso ($K = .702$, $p < .001$), upper torso ($K = .630$, $p < .001$), lower leg ($K = .749$, $p < .001$), and foot ($K = .722$, $p < .001$) scores. Upper arm scores had the least concordance, being categorized as "fair" in agreement level ($K = .382$, $p = .006$). This is likely due to the outline of the posterior side of the upper arm, the most consistently visible marker for the limb, being obscured by the monkey's long fur and blending into its torso.

One observer (L.O.C) also scored mount stability duration for the entire data set, thus intra-rater reliability was assessed by re-scoring another 30 randomly selected mounts. An intra-class correlation score of .96 was reached, signifying an "excellent"

agreement (Cicchetti & Sparrow, 1981) and thus consistent scoring of mount stability duration.

Results

The heterosexual group was comprised of 13 individuals who collectively performed 49 mounts, and the homosexual group was comprised of 13 individuals who collectively performed 90 mounts. Thirty Fisher's Exact tests of independence, each with $N = 26$ (13 heterosexual, 13 homosexual), were conducted for each of the eight body segments. Seven of the eight limbs did not differ in positioning between the homosexual and heterosexual groups, as they did not yield a statistically significant Fisher value. The lower leg was the only segment to show a significant difference between the groups, for which significance occurred once out of the 30 testing trials. A binomial test showed that this result differed significantly ($p < .001$) from a null model that predicted equal significant and non-significant Fisher values. Therefore, the binomial test indicated that there was no difference between the two groups for the lower leg. Fisher's Exact test values for all 30 trials are presented in Table 3.2.

Discussion

Japanese macaques are unique in their sexual behaviour, as females of this species are known to mount both males *and* females in some populations. While a functional approach offers a partial explanation for the existence this phenomenon, these two forms of non-conceptive sexual mounts can only be comprehensively understood by investigating the evolutionary events that lead to their modern-day form. To do so, a step-by step reconstruction of the behaviours' historical pathway must be composed, with each hypothesized event being reinforced by evidence (Vasey, 2007; for a more general

discussion of these ideas pertaining to the evolutionary history of behaviour, see Alcock, 1989).

Vasey's (2002a; VanderLaan et al., 2012) 4-step model of the evolutionary history of non-conceptive mounting in female Japanese macaques posits that (1) the mounting between males originated as an attention-getting behavioural pattern during social play sessions among juveniles, (2) sexually motivated females exploited this behaviour and began mounting males in an adaptive capacity to entice them to mount in return, (3) females eventually evolved the ability to obtain sexual reward from female-male mounting, and (4) as a functionless by-product of male mounting, females subsequently evolved the ability to mount females, which provided alternate means to gain sexual stimulation. Ultimately, both forms of female mounting are hypothesized to be closely phylogenetically linked. Female-male mounting, a likely adaptive behaviour, would be the necessary precursor of female-female mounting, a functionless by-product motivated solely by the pursuit of sexual reward. Claims about both forms of mounting have received evidentiary support (Chapter 2; Gouzoules & Goy, 1983; Vasey, 1995, 1996, 1998, 2004a; Vasey et al., 1998).

In this chapter, I aimed to shed further light on the proposed phylogenetic link between female-male and female-female mounting by comparing specific structural components that mounters employ during both forms of mounting. To do so, the position of mounters' body segments in space (lower torso, mid torso, upper torso, upper arm, lower arm, upper leg, lower leg, and foot) during female-male and female-female mounting were measured and compared. No significant difference in the positioning of

any of the eight body segments was found between female-male and female-female mounters, supporting the hypothesis of their evolutionary relatedness.

This result is particularly compelling when considering the observed covariational pattern of both forms of mounting. Specifically, Leca et al. (2014b) found that across populations of Japanese macaques, female-female mounting does not exist in the absence of female-male mounting, implying that the latter is a necessary precursor for the emergence of the former. Together, these results support the notion that both behaviours are phylogenetically related, with female-male mounting being the necessary (and adaptive) precursor, and female-female mounting being its facultative by-product, thus supporting Vasey's model for the evolution of non-conceptive mounting behaviour in this species.

The striking similarities found between female-male and female-female mounting also raises questions regarding their level of evolutionary relatedness. Using the same logic used to explain genetic similarities among closely related species (e.g. Gordân, Narlikar, & Hartemink, 2010) and divergent populations (e.g. Harris & Taylor, 2010), the structural likeness between the two mounting behaviours may be due to female-female mounting being a derived behaviour. In other words, in terms of mounters' limb orientation, female-female mounting may have evolved from female-male mounting too recently to have had a chance to diversify from its precursory behaviour.

While the lack of differences between the two forms of mounting further bolsters the proposed hypothesis, it is important to note that the occurrence of differences would not have falsified it. Instead, it may have informed us about certain ultimate and proximate elements that contribute to the behaviours' expression, and it is arguably

surprising that not a single difference was found between the two mount forms. If female-male mounting is an adaptation, it is subject to high selection pressures to maintain an optimal fitness-enhancing form. In addition to being a neutral by-product, female-female mounting is also not an *immediate* consequence of the adaptation, as it does not always co-exist with female-male mounting within populations (Leca et al., 2014b). Its lack of fitness consequences in addition to its "loose" association with the precursory adaptation means that female-female mounting is not functionally constrained, which should allow for the emergence of more flexible, diverse and arbitrary limb positions. This variety could be explained in terms of motivation to seek sexual reward (Vasey & Duckworth, 2006; Vasey et al., 2008), with an unrestricted range in limb positions allowing more effective VPA stimulation. Moreover, structural differences between female-male and female-female mounts could have been explained in terms of the differing level of risk associated with each form of mounting. Given that heterosexually consorting females are more susceptible to aggression and injury than those in homosexual consortships (Gunst et al., 2015), female mounters could be more apprehensive when atop a male, perhaps positioning themselves in a manner that would facilitate rapid dismount upon receiving a threat.

Overall, the lack of differences between mounting positions in both forms of mounting is congruent with the hypothesis of their evolutionary relatedness, but the lack of differences is arguably curious. While the *motionless* body segment positions that are held during female-male and female-female mounting do not differ, other aspect of the behaviours, such as movement, duration, or associations with other behaviours, may differ in some way, with the aforementioned mechanisms offering possible explanations

for their existence (e.g. difference in the diversity and complexity of movements between

female-female and male-female mounting, Vasey et al., 2006).

Table 3.1. Number of mounts per individual within the heterosexual and homosexual mounting categories

	Mounter name	Number of mounts
Heterosexual category	Ai-61-72-83	1
	Co-65-71-87	1
	Co-65-81	4
	Co-65-81-89	22
	Ko-62-72-77-85	1
	Me-62-80-91	3
	Mi-63-75	1
	Mi-63-75-80-89-94	8
	Mi-63-75-83	1
	Mi-63-75-93	1
	Mi-63-75-93-98	1
	Mi-82-91	3
	Shi-62-67-79-85-96-03	2
Homosexual category	Co-65-71-87-93	5
	Co-65-71-90-01	1
	Co-65-81-94	2
	Co-65-81-94-01	1
	Ko-62-74-84	4
	Ku-59-71-76-87-01	14
	Mi-63-69-74-90-95	2
	Mi-63-75-80	18
	Mi-63-75-80-89-98	2
	Mi-82	22
	Mo-59-78-92-99	9
	Mo-59-78-92-99-04	2
	Yun-76-81-89-96	8

Table 3.2. Fisher's Exact test values obtained when comparing the EWMN positions of eight body segments in females performing heterosexual and homosexual mounts

	Body segments							
	Lower torso	Mid torso	Upper torso	Upper arm	Lower arm	Upper leg	Lower leg	Foot
Trial 1	χ^2 = .84 p = .018 df = 3	χ^2 = 2.33 p = 1.00 df = 2	χ^2 = 1.58 p = .509 df = 2	χ^2 = 1.38 p = .695 df = 2	χ^2 = 3.06 p = .467 df = 3	χ^2 = .46 p = 1.00 df = 2	χ^2 = 3.41 p = .673 df = 4	χ^2 = 1.67 p = .813 df = 3
Trial 2	χ^2 = 5.80 p = .073 df = 3	χ^2 = 1.87 p = 1.00 df = 2	χ^2 = .33 p = 1.00 df = 2	χ^2 = 1.38 p = .695 df = 2	χ^2 = .47 p = 1.00 df = 2	χ^2 = 1.66 p = .532 df = 2	χ^2 = 5.36 p = .160 df = 4	χ^2 = 7.75 p = .026 df = 2
Trial 3	χ^2 = 2.75 p = .50 df = 3	χ^2 = 2.11 p = 1.00 df = 3	χ^2 = .59 p =1.00 df = 2	χ^2 = 1.10 p = 1.00 df = 2	χ^2 = .688 p = 1.00 df = 2	χ^2 = 1.43 p = .688 df = 2	χ^2 = 4.46 p =.322 df = 4	χ^2 = 2.22 p = .767 df = 3
Trial 4	χ^2 = 3.05 p = .551 df = 3	χ^2 = 1.87 p = 1.00 df = 2	χ^2 = .33 p = 1.00 df = 2	χ^2 = 1.08 p = 1.00 df = 2	χ^2 = .50 p = 1.00 df = 2	χ^2 = .46 p = 1.00 df = 2	χ^2 = 6.47 p = .073 df = 4	χ^2 = 10.25 p = .004 df = 3
Trial 5	χ^2 = 3.15 p = .378 df = 3	χ^2 = 2.33 p = 1.00 df = 3	χ^2 = 1.95 p = .528 df = 2	χ^2 = 1.10 p = 1.00 df = 2	χ^2 = 1.79 p = .688 df = 2	χ^2 = .87 p = .866 df = 2	χ^2 = 6.47 p = .073 df = 4	χ^2 = 2.97 p = .410 df = 3
Trial 6	χ^2 = 4.27 p = .326 df = 4	χ^2 = 1.22 p = 1.00 df = 2	χ^2 = .70 p = 1.00 df = 2	χ^2 = 1.38 p = .695 df = 2	χ^2 = 1.94 p = .580 df = 2	χ^2 = .79 p = .776 df = 2	χ^2 = 9.39 p = .015 df = 4	χ^2 = 3.08 p = .440 df = 3
Trial 7	χ^2 = 6.57 p = .069 df = 4	χ^2 = 4.61 p = .096 df = 3	χ^2 = .56 p =1.00 df = 2	χ^2 = .31 p = 1.00 df = 2	χ^2 = 3.34 p = .202 df = 2	χ^2 = .46 p = 1.00 df = 2	χ^2 = 4.78 p = .234 df = 4	χ^2 = 3.14 p = .366 df = 3

| Trial								
8	$\chi^2 = 5.22$ $p = .110$ $df = 4$	$\chi^2 = 1.87$ $p = 1.00$ $df = 2$	$\chi^2 = .90$ $p = .720$ $df = 2$	$\chi^2 = 1.06$ $p = 1.00$ $df = 2$	$\chi^2 = 2.67$ $p = .249$ $df = 2$	$\chi^2 = .46$ $p = 1.00$ $df = 2$	$\chi^2 = 9.33$ $p = .014$ $df = 4$	$\chi^2 = 4.00$ $p = .177$ $df = 2$
9	$\chi^2 = 3.88$ $p = .160$ $df = 2$	$\chi^2 = 2.03$ $p = .480$ $df = 2$	$\chi^2 = 1.37$ $p = .787$ $df = 2$	$\chi^2 = 1.07$ $p = 1.00$ $df = 2$	$\chi^2 = 2.07$ $p = .446$ $df = 2$	$\chi^2 = .47$ $p = 1.00$ $df = 2$	$\chi^2 = 9.33$ $p = .014$ $df = 4$	$\chi^2 = 4.32$ $p = .129$ $df = 2$
10	$\chi^2 = 3.65$ $p = .288$ $df = 3$	$\chi^2 = 1.22$ $p = 1.00$ $df = 2$	$\chi^2 = .62$ $p = 1.00$ $df = 2$	$\chi^2 = 2.02$ $p = .428$ $df = 2$	$\chi^2 = 1.38$ $p = 1.00$ $df = 3$	$\chi^2 = .20$ $p = 1.00$ $df = 2$	$\chi^2 = 5.36$ $p = .160$ $df = 4$	$\chi^2 = 3.10$ $p = .379$ $df = 3$
11	$\chi^2 = 3.51$ $p = .397$ $df = 3$	$\chi^2 = 1.87$ $p = 1.00$ $df = 2$	$\chi^2 = .69$ $p = 1.00$ $df = 2$	$\chi^2 = 1.38$ $p = .695$ $df = 2$	$\chi^2 = 1.43$ $p = .688$ $df = 2$	$\chi^2 = .31$ $p = 1.00$ $df = 2$	$\chi^2 = 3.53$ $p = .645$ $df = 4$	$\chi^2 = 3.59$ $p = .160$ $df = 2$
12	$\chi^2 = 3.05$ $p = .230$ $df = 2$	$\chi^2 = 1.22$ $p = 1.00$ $df = 2$	$\chi^2 = 1.38$ $p = .787$ $df = 2$	$\chi^2 = 1.08$ $p = 1.00$ $df = 2$	$\chi^2 = 2.10$ $p = 1.00$ $df = 3$	$\chi^2 = .87$ $p = .866$ $df = 2$	$\chi^2 = 11.15$ $p = .004$ $df = 4$	$\chi^2 = 2.59$ $p = .371$ $df = 2$
13	$\chi^2 = 1.21$ $p = 1.00$ $df = 2$	$\chi^2 = 2.03$ $p = .480$ $df = 2$	$\chi^2 = 1.27$ $p = .720$ $df = 2$	$\chi^2 = 4.07$ $p = .115$ $df = 2$	$\chi^2 = 1.08$ $p = 1.00$ $df = 2$	$\chi^2 = 1.71$ $p = .590$ $df = 2$	$\chi^2 = 4.46$ $p = .322$ $df = 4$	$\chi^2 = 3.11$ $p = .272$ $df = 2$
14	$\chi^2 = 2.39$ $p = .673$ $df = 3$	$\chi^2 = 2.33$ $p = 1.00$ $df = 3$	$\chi^2 = 1.14$ $p = .720$ $df = 2$	$\chi^2 = 2.020$ $p = .428$ $df = 2$	$\chi^2 = 1.88$ $p = .753$ $df = 3$	$\chi^2 = 1.85$ $p = .532$ $df = 2$	$\chi^2 = 11.07$ $p = .005$ $df = 4$	$\chi^2 = 5.31$ $p = .083$ $df = 2$
15	$\chi^2 = 5.21$ $p = .073$ $df = 2$	$\chi^2 = 2.61$ $p = .480$ $df = 2$	$\chi^2 = .56$ $p = 1.00$ $df = 2$	$\chi^2 = 1.38$ $p = .695$ $df = 2$	$\chi^2 = 1.061$ $p = 1.00$ $df = 2$	$\chi^2 = .31$ $p = 1.00$ $df = 2$	$\chi^2 = 7.00$ $p = .048$ $df = 4$	$\chi^2 = 8.75$ $p = .009$ $df = 3$
16	$\chi^2 = 3.15$ $p = .378$ $df = 3$	$\chi^2 = 2.33$ $p = 1.00$ $df = 3$	$\chi^2 = .59$ $p = 1.00$ $df = 2$	$\chi^2 = 1.38$ $p = .695$ $df = 2$	$\chi^2 = 1.76$ $p = .827$ $df = 3$	$\chi^2 = .56$ $p = 1.00$ $df = 2$	$\chi^2 = 5.75$ $p = .113$ $df = 4$	$\chi^2 = 2.97$ $p = .410$ $df = 3$

Trial								
17	$\chi^2 = 2.75$ $p = .504$ $df = 3$	$\chi^2 = 2.11$ $p = 1.00$ $df = 3$	$\chi^2 = 1.40$ $p = .645$ $df = 2$	$\chi^2 = 2.83$ $p = .238$ $df = 2$	$\chi^2 = 6.38$ $p = .039$ $df = 2$	$\chi^2 = .87$ $p = .754$ $df = 2$	$\chi^2 = 4.03$ $p = .378$ $df = 4$	$\chi^2 = .54$ $p = 1.00$ $df = 2$
18	$\chi^2 = 5.22$ $p = .110$ $df = 3$	$\chi^2 = 4.61$ $p = .096$ $df = 3$	$\chi^2 = .62$ $p = 1.00$ $df = 2$	$\chi^2 = 4.43$ $p = .162$ $df = 3$	$\chi^2 = 1.46$ $p = .506$ $df = 2$	$\chi^2 = .94$ $p = .834$ $df = 2$	$\chi^2 = 3.53$ $p = .645$ $df = 4$	$\chi^2 = 10.31$ $p = .009$ $df = 3$
19	$\chi^2 = 8.44$ $p = .018$ $df = 3$	$\chi^2 = 2.61$ $p = .480$ $df = 2$	$\chi^2 = .50$ $p = 1.00$ $df = 2$	$\chi^2 = 2.15$ $p = .411$ $df = 2$	$\chi^2 = 1.89$ $p = .673$ $df = 2$	$\chi^2 = .55$ $p = 1.00$ $df = 3$	$\chi^2 = 13.15$ $p = .002$ $df = 4$	$\chi^2 = 4.36$ $p = .095$ $df = 3$
20	$\chi^2 = 4.34$ $p = .245$ $df = 3$	$\chi^2 = 3.17$ $p = .486$ $df = 3$	$\chi^2 = 1.08$ $p = 1.00$ $df = 2$	$\chi^2 = 1.32$ $p = 1.00$ $df = 3$	$\chi^2 = 2.91$ $p = .221$ $df = 2$	$\chi^2 = .55$ $p = 1.00$ $df = 2$	$\chi^2 = 3.53$ $p = .645$ $df = 4$	$\chi^2 = 2.30$ $p = .641$ $df = 3$
21	$\chi^2 = 3.05$ $p = .551$ $df = 3$	$\chi^2 = 3.68$ $p = .344$ $df = 3$	$\chi^2 = .69$ $p = 1.00$ $df = 2$	$\chi^2 = .47$ $p = 1.00$ $df = 2$	$\chi^2 = 1.96$ $p = .591$ $df = 2$	$\chi^2 = 1.061$ $p = 1.00$ $df = 2$	$\chi^2 = 5.36$ $p = .160$ $df = 4$	$\chi^2 = 1.40$ $p = .680$ $df = 2$
22	$\chi^2 = 5.22$ $p = .110$ $df = 3$	$\chi^2 = 1.04$ $p = 1.00$ $df = 2$	$\chi^2 = .46$ $p = 1.00$ $df = 2$	$\chi^2 = 1.95$ $p = .434$ $df = 2$	$\chi^2 = 1.71$ $p = .533$ $df = 2$	$\chi^2 = .92$ $p = .751$ $df = 2$	$\chi^2 = 6.99$ $p = .065$ $df = 4$	$\chi^2 = 3.10$ $p = .379$ $df = 3$
23	$\chi^2 = 4.34$ $p = .245$ $df = 3$	$\chi^2 = 3.00$ $p = .451$ $df = 3$	$\chi^2 = .33$ $p = 1.00$ $df = 2$	$\chi^2 = 1.68$ $p = .834$ $df = 3$	$\chi^2 = 2.77$ $p = .580$ $df = 3$	$\chi^2 = 3.79$ $p = .166$ $df = 2$	$\chi^2 = 4.03$ $p = .378$ $df = 4$	$\chi^2 = 2.12$ $p = .579$ $df = 3$
24	$\chi^2 = 4.80$ $p = .156$ $df = 3$	$\chi^2 = 2.85$ $p = 1.00$ $df = 3$	$\chi^2 = .59$ $p = 1.00$ $df = 2$	$\chi^2 = 1.43$ $p = .688$ $df = 2$	$\chi^2 = 1.12$ $p = .813$ $df = 2$	$\chi^2 = .46$ $p = 1.00$ $df = 2$	$\chi^2 = 11.07$ $p = .005$ $df = 4$	$\chi^2 = 2.92$ $p = .341$ $df = 2$
25	$\chi^2 = 1.96$ $p = 1.00$ $df = 3$	$\chi^2 = 2.85$ $p = 1.00$ $df = 3$	$\chi^2 = .90$ $p = .720$ $df = 2$	$\chi^2 = 1.38$ $p = .695$ $df = 2$	$\chi^2 = 1.54$ $p = 1.00$ $df = 3$	$\chi^2 = 1.067$ $p = 1.00$ $df = 2$	$\chi^2 = 7.90$ $p = .039$ $df = 4$	$\chi^2 = 1.37$ $p = .787$ $df = 2$

Trial								
26	$\chi^2 = 4.19$ $p = .196$ $df = 3$	$\chi^2 = 1.52$ $p = .593$ $df = 2$	$\chi^2 = .83$ $p = 1.00$ $df = 2$	$\chi^2 = 1.07$ $p = 1.00$ $df = 2$	$\chi^2 = 1.79$ $p = .688$ $df = 2$	$\chi^2 = .92$ $p = .751$ $df = 2$	$\chi^2 = 6.47$ $p = .073$ $df = 4$	$\chi^2 = 4.32$ $p = .129$ $df = 2$
27	$\chi^2 = 3.65$ $p = .288$ $df = 3$	$\chi^2 = 1.35$ $p = 1.00$ $df = 2$	$\chi^2 = 1.14$ $p = 1.00$ $df = 2$	$\chi^2 = 1.14$ $p = 1.00$ $df = 2$	$\chi^2 = 1.06$ $p = 1.00$ $df = 2$	$\chi^2 = 1.46$ $p = .590$ $df = 2$	$\chi^2 = 15.11$ $p =.001^*$ $df = 4$	$\chi^2 = 1.25$ $p = 1.00$ $df = 3$
28	$\chi^2 = 2.43$ $p = .688$ $df = 3$	$\chi^2 = 1.35$ $p = 1.00$ $df = 2$	$\chi^2 = 1.37$ $p = .787$ $df = 2$	$\chi^2 = 1.07$ $p = 1.00$ $df = 2$	$\chi^2 = 1.65$ $p = .645$ $df = 2$	$\chi^2 = 3.79$ $p = .166$ $df = 2$	$\chi^2 = 6.11$ $p = .103$ $df = 4$	$\chi^2 = 0.22$ $p = 1.00$ $df = 2$
29	$\chi^2 = 3.65$ $p = .288$ $df = 3$	$\chi^2 = 3.68$ $p = .344$ $df = 3$	$\chi^2 = .90$ $p = .720$ $df = 2$	$\chi^2 = 1.08$ $p = 1.00$ $df = 2$	$\chi^2 = 1.76$ $p = .548$ $df = 2$	$\chi^2 = .87$ $p =.754$ $df = 2$	$\chi^2 = 5.36$ $p = .160$ $df = 4$	$\chi^2 = 7.53$ $p = .019$ $df = 2$
30	$\chi^2 = 2.13$ $p = 1.00$ $df = 3$	$\chi^2 = 1.52$ $p = .593$ $df = 2$	$\chi^2 = 1.019$ $p = .680$ $df = 2$	$\chi^2 = 1.38$ $p = .695$ $df = 2$	$\chi^2 = 1.34$ $p = .688$ $df = 2$	$\chi^2 = 1.38$ $p = .520$ $df = 2$	$\chi^2 = 4.034$ $p = .378$ $df = 4$	$\chi^2 = 1.88$ $p = .509$ $df = 2$

* $p = .001$
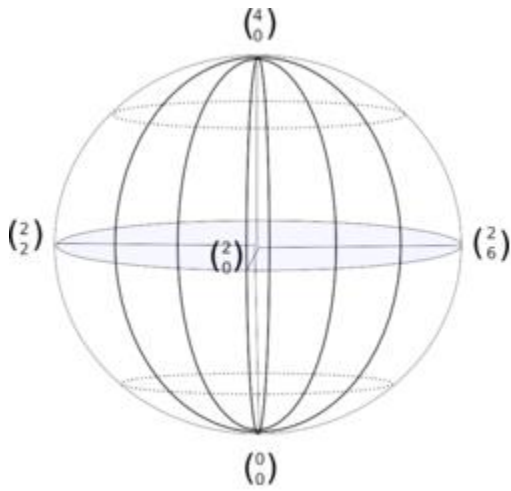
Figure 3.1. Three-dimensional EWMN sphere
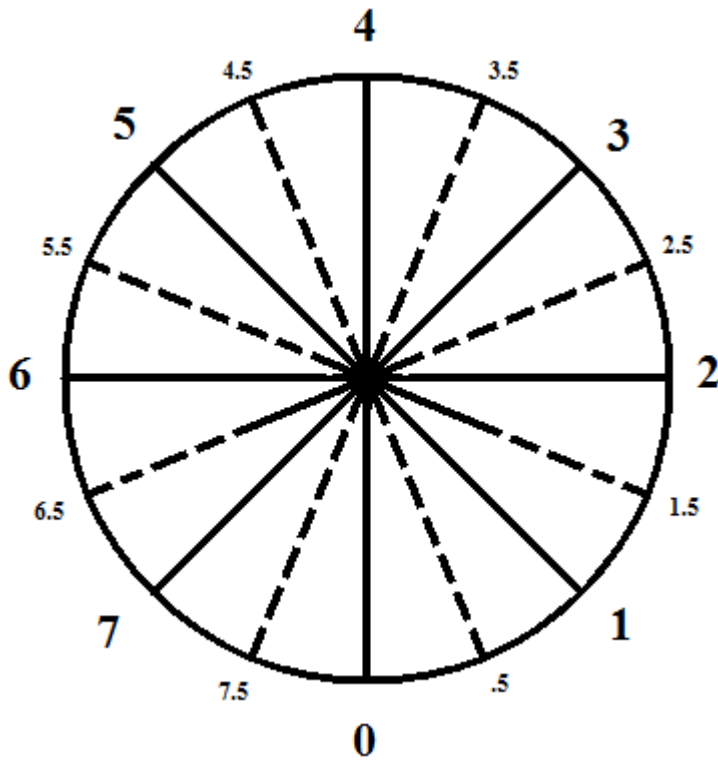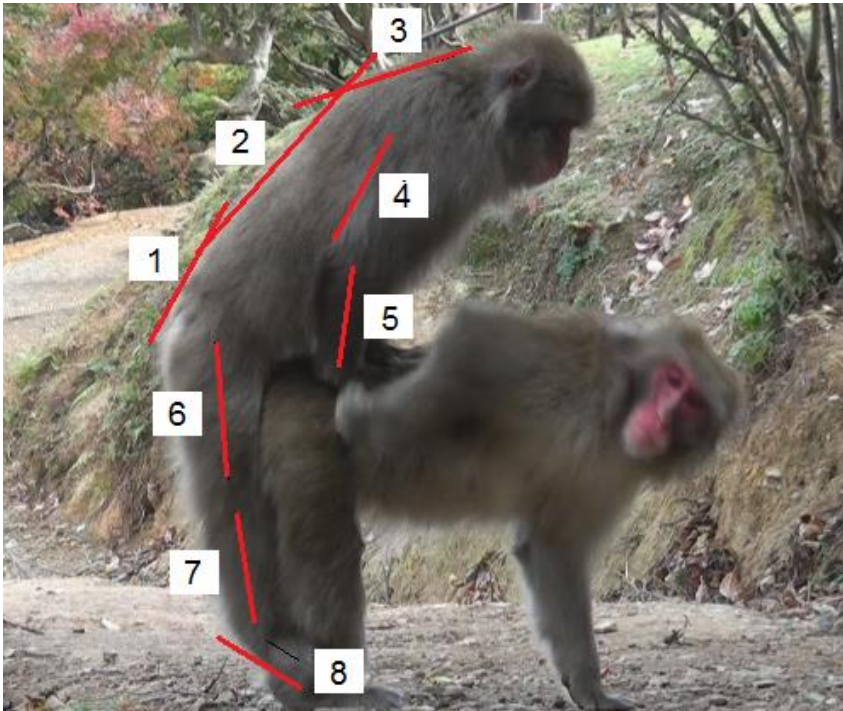Adapted from "EWMN system of reference" courtesy of Wikipedia user Onsat2003, 2008.

Figure 3.2. Two-dimensional EWMN sphere

Figure 3.3. Approximate location of eight measured body segments

CHAPTER FOUR

Conclusion: Future Directions and Limitations

At first glance, non-conceptive sex may appear to be a conundrum, as it is comprised of sexual interactions that are typically expressed during heterosexual courtship and consortships, yet they do not directly contribute to the functional goal of reproduction. Japanese macaques are a unique species in this respect, as adult females in certain populations partake in *two* forms of non-conceptive mounting: female-male and female-female mounting. Both occur during temporary but exclusive sexual partnerships known as heterosexual and homosexual consortships, and both are associated with a similar repertoire of courtship behaviours (Vasey, 2002a). Moreover, both forms of mounting are underlain by similar female sex hormone profiles (O'Neill et al., 2004b). However, while female-female mounting does not have potentially reproductive implications, female-male mounting likely does.

In line with this, female-male mounting in this species is likely a proceptive behaviour, hypothesized to function as a prompt for sluggish males to mount the sexually proceptive females that mount them (Vasey, 2002a, 2006, 2007; for a more general discussion regarding mammal species, see Beach, 1968, 1976). However, despite 30 years of research on this topic (Leca et al., 2015), female-female mounting in Japanese macaques does not appear to be adaptive (Vasey, 2004b). The overwhelming lack of evidence for a function for this behaviour strongly implies that female-female mounting is a functionless by-product of the purportedly adaptive female-male mounting (Vasey, 2002a, 2006; VanderLaan et al., 2012). This notion is supported by the intergroup covariation pattern of both forms of mounting in this primate species (Leca et al., 2014b).

As expected, female-female mounting only occurs in groups where female-male mounting was also present. Further research was needed, however, to solidify the hypothesized evolutionary relationship between both forms of mounting. While female-female mounting is not adaptive, it is sexual, and largely driven by proximate sexual reward (Vasey & Duckworth, 2006; Vasey et al., 2006). Female-male mounting also involves proximate erotic stimulation (Vasey & Duckworth, 2008). However, additional proximate triggers that are relevant to its adaptive nature, such as male departure from the female consort partner (Vasey, 2002a), had yet to be empirically investigated.

With these findings and hypotheses in mind, this thesis had two objectives. First, as female-male mounting has been significantly less studied than female-female mounting in this species, I aimed to gain an overall better understanding of the former by investigating the proximate and ultimate forces driving this mounting behaviour. Second, while some evidence exists to suggest a phylogenetic relationship between these two forms of mounting (e.g., Leca et al., 2014b), I aimed to gain a further understanding of the hypothesized relationship between them.

In Chapter 2, I investigated two forces responsible for the evolution and expression of female-male mounting in Japanese macaques, namely the behaviour's adaptive function and the proximate triggers that stimulate the behaviour. First, the adaptive utility of female-male mounting was tested by examining male mounting activity following female-male mounts. In line with Vasey's (2002a, 2006, 2007) species-specific hypothesis, and in a broader sense, Beach's (1968, 1976) mammal-wide claim, I found that female-male mounts were associated with both a greater likelihood, and an increased rate, of subsequent male mounts, suggesting that the behaviour functions to

prompt male-female mounting. Second, to identify the proximate mechanisms driving

female-male mounting, I focussed on the dyadic interactions that occurred prior to this

sexual behaviour, and examined the order of the movements and actions employed by

male and female consort partners during female-male mounting sequences. I found a total

of seven female-male mounting sequence categories, with each one being initiated by

female movement (Categories #1, #2 and #3), male movement (Categories #4, #5, and

#6), or an unclear initiator (Category #7). The occurrence of male-initiated sequences

clearly showed that females mount in response to male movement (see Vasey, 2002a for

previous anecdotal reports), and are sensitive to both large and small-scale male

movements. However, the fact that 79% of observed mounting sequences were initiated

by females strongly suggests that female-male mounting is largely driven by internal

female motivation instead of external male-induced stimuli. During the female-initiated

sequences, males responded positively to both the explicit sexual hand-on-hindquarters

signal, and the incidental by-product body movements (i.e. *cues*), expressed during the

execution of this signal (e.g. the female reorienting her body and reaching for the male's

hindquarters). This demonstrates that males anticipate and facilitate the execution of

female-male mounts, by being responsive to both signals and cues related to imminent

female mounting.

In Chapter 3, I further investigated the phylogenetic relationship between female-

male and female-female mounting. To do so, I used the Eshkol-Wachman Movement

Notation to measure and compare the body segment positions that female mounters

employ during both forms of mounting. I found no differences in of any of the eight body

segments positions between both forms of mounting, thus supporting the hypothesis of

70

their evolutionary relationship. While these results fit well with the covariation pattern of female mounting across Japanese macaque populations (Leca et al., 2014b), the complete lack of differences was also surprising. Indeed, female-female mounting (i.e. a functionless by-product) is not likely to be constrained by the same selective pressures as those acting upon female-male mounting (i.e. an adaptation). Therefore, it would not have been surprising if the former had been slightly more variable in its form than the latter.

The results and conclusions attained in this thesis have furthered our knowledge regarding the function, proximate triggers, and evolutionary history of non-conceptive mounting in Japanese macaques. However, they also raise further questions and suggest future research directions in this domain.

Considerations of Future Directions and Limitations

The missing step in the phylogenetic model. According to Vasey's model, non-conceptive mounting in female Japanese macaques arose via four distinct steps, with various amounts of current-day behavioural evidence supporting each one (Step 1: Gunst et al., 2013; Step 2: Chapter 2; Step 3: Vasey & Duckworth, 2008; Step 4: Chapter 3; Vasey & Duckworth, 2006; Vasey et al., 2006). However, I would argue that a significant knowledge gap exists between Step 1 (i.e. males are primed to be mounted and to respond to mounting through the customary male-male mounting during juvenile social play) and Step 2 (i.e. females "exploited this evolutionary loophole" [Vasey, 2002a, p.173] by evolving the ability to mount males) of the model. In other words, what evolutionary stepping-stones led to females gaining the ability to mount males?

In male Japanese macaques, non-kin-directed mounting behaviour emerges in, and persists throughout, the juvenile period (1-3 years of age) (Gunst et al., 2013; Hanby & Brown, 1974). During this time, mounting is employed as a component of male-male social play (VanderLaan et al., 2012), may function as a tension-reducing behaviour during stressful events (Gunst et al., 2013; VanderLaan et al., 2012), and is employed in a strictly sexual sense, with males as young as 2 years of age partaking in fully-realized consortships with adult females (Gunst et al., 2013), despite their inability to ejaculate before 4 years of age (Hanby & Brown, 1974). The juvenile period is critical to the development of male heterosexual mounting (Gunst et al., 2013) and other male sexual behaviours, including homosexual mounting (Leca et al., 2014c). During development, male mounting behaviour "improves" and becomes more adult-like with every passing year. This includes increased frequencies in overall mounting, as well as, more double foot-clasp mounts and mounts conducive to intromission (Gunst et al., 2013). In contrast, females appear to lack this early-starting and extensive "practice period", as their juvenile period (1-2 years old) is characterized by very little mounting, especially compared to males (Gunst et al., 2013). Instead, females begin their sexual "mounting career" upon their first oestrus, which occurs at 3 years of age (Hanby & Brown, 1974; Wolfe, 1978; Leca et al., 2014a). However, during this time, as well as throughout the rest of their adolescent period (3-4 years old), females primarily mount (and are solicited by) adult *females* (Leca et al., 2014d). This may be the result of two factors: (1) adult males are largely disinterested in adolescent females as consort partners, and (2) females are less likely to be aggressed and/or harmed by their consort partners and/or third party individuals when they partake in homosexual consortships than when engaged in

heterosexual consortships (Gunst et al., 2015). It is not until females reach adulthood (≥ 5 years of age) that female-male mounting is more routinely observed (Leca et al., 2014d).

Given this, can it be said that, from a developmental perspective, female Japanese macaques acquire the ability to mount males by first mounting females during their adolescence? Perhaps. Play, for example, may function as a means of acquiring important fitness-relevant skills needed during adulthood, namely agonistic and predatory ones (Smith, 1982). In a similar manner, perhaps homosexual mounting in female Japanese macaques during the adolescent period *facilitates* the occurrence of female-male mounting in adulthood. To test this, future studies on this topic would have to directly compare the frequency of females' homosexual mounting during adolescence to their frequency of female-male mounting in adulthood. Furthermore, such a modern-day utility would make female-female mounting an *exaptation*, that is, a feature that was originally functionless but was later co-opted for a specific utility (Buss et al., 1998; Gould & Vrba, 1982).

In a phylogenetic sense, however, female-female mounting was likely not the evolutionary precursor of female-male mounting in Japanese macaques. Fundamental to the relationships between adaptations and their by-products, female-male mounting would pre-date female-female mounting (Vasey, 2002a, 2006, 2007). Therefore, female-female mounting could not have led to female-male mounting, and thus cannot be the missing evolutionary step between Step 1 and Step 2 of Vasey's model. Overall, the study of the phylogeny of non-conceptive mounting in female Japanese macaques is complex, in part due to the opposing historical timelines of the emergence of female-male and female-female mounting. Specifically, from a developmental perspective, female-

female mounting appears earlier than female-male mounting, whereas from an evolutionary viewpoint, female-male mounting seems to have preceded female-female mounting.

However, a species-specific present-day behaviour that may have played a precursory role in the emergence of female-male mounting is non-sexual mounting during infancy. Japanese macaque infants of both sexes mount in a "boarding style" fashion, which involves clinging to, and mounting upon, their mothers' (and other female kins') hindquarters and lower backs during locomotion (Hanby & Brown, 1974). While this type of mounting is only observed during infancy (0-1 years old), perhaps it acted as the necessary precursor for females to gain the ability to mount males later in the species' evolutionary history. Future investigations into this possibility should seek if a link exists between female infant boarding and subsequent female-male mounting in adulthood. While both infant male and female boarding-style mounts have been described as "undifferentiated", such observations have been in reference to a single population (in which both adult female-male and female-female mounting occurred; Hanby & Brown, 1974). An inter-group comparison of infant mounting, with effort put into obtaining data from populations with various levels of female-male mounting, may help to uncover a relationship between boarding mounts performed by infant females and adult female-male mounting.

Furthermore, comparisons of infant, juvenile, and adolescent behaviour across many macaque species may shed some light on the existence of interactions that are conducive to female-male mounting in adulthood. Aside from mounting itself, other interactions, such as social play (Shimada, 2006) and clasping/embracing behaviour

(Nakagawa et al., 2015), may be worthy of investigation, as their dyadic and tactile natures may facilitate the expression of female-male mounting. Comparing the expression of such behaviours across macaque species that do (e.g. rhesus (*Macaca mulatta*), pig-tailed (*Macaca nemestrina*), and long-tailed macaques (*Macaca fascicularis*): Dagg, 1984) and do not (e.g. tonkean (*Macaca tonkeana*), lion-tailed (*Macaca silenus*), and Heck's macaques (*Macaca hecki*) exhibit female-male mounting in adulthood could allow us to better understand the origin and evolution of female-male mounting within the genus *Macaca*. Furthermore, if hypothesized mounting-relevant behaviours are found to exist in macaque species exhibiting female-male mounting but *not* in Japanese macaques, it could be argued that these mounting-relevant behaviours may have been present in the Japanese macaque's evolutionary past but are no longer extant today. Such an outcome could provide possible evolutionary precursors to adult female-male mounting.

Indeed, cross-species comparative research often holds the key to the origins and evolutionary history of behavioural patterns that evade typical functional analyses (Alcock, 1989; Gould, 1986). Moreover, the genus *Macaca* is an ideal candidate for phylogenetic studies of behaviour, as its species members display a large amount of inter-specific variation that is unparalleled by any other primate taxa (Thierry, Iwaniuk, & Pellis, 2000). The high level of variety in species-specific traits, such as aggression, socialization, temperament, and dominance hierarchy types, provides many comparative points by which to determine the phylogenetic origins and pathways of these social behaviours (Thierry et al., 2000).

Differences between mount types and their effects. In the Arashiyama-E troop, female Japanese macaques perform five distinct mount types. Double foot-clasp, sitting, and reclining mounts are those most commonly performed during both homosexual and heterosexual consortships, whereas standing and ventro-ventral mounts are comparably rare in both contexts (Leca et al., 2014b; Vasey & Duckworth, 2006; Vasey & Reinhart, 2009; Vasey et al., 2006). In the current study, correlations between mount types and male behaviour, as well as the structural differences between both forms of mounting for other mount types, were not explored. Further research on this subject is, therefore, warranted.

In Chapter 2, the overall sample size ($N = 100$ mounts) and the small number of individuals sampled ($N = 10$) contributed to the small range of mount types observed, thus reducing the representativeness of the data, as only double foot-clasp and reclining mounts were observed. While this question has never been investigated or raised in the literature, future research on the topic should determine whether different types of mounts are related to, or performed in response to, certain social factors, serve different functions, or communicate different messages to the mounted male. For example, the double foot-clasp mount is the most commonly used mount type among male juveniles (VanderLaan et al., 2012). It has been postulated that this mount type is optimal with respect to obtaining mountees' attention during play, as it involves making physical contact with four distinct body regions, and may thus maximize the salience of the behaviour to the mountee (VanderLaan et al., 2012). These same principles of effective communication (Wiley, 2006) can also be potentially used to explain female-male

mounting, particularly when considering the type of tactile sensation that males receive when being mounted.

In females, reclining mounts appear to be the most contact-heavy mount, as almost their entire torso is collapsed onto the male's back. While all mount types likely weigh down or slow down the male to some extent, reclining mounts are arguably the most heavily felt by males. Therefore, this mount type may be the most effective in impeding male movement, a functional component of this behavioural pattern that would be particularly useful when males begin to move or successfully remove themselves from females' immediate vicinities (i.e. Category #4 and #5 mount sequences). Additionally, a female-male double foot-clasp mount, which likely affords males the greatest amount of direct genital stimulation out of all the mount types, may be the most effective manoeuver to sexually stimulate a male that is stationary yet sexually inactive towards the female.

In the same line of inquiry, future research should also consider the effects of (overall and different types of) mounting on the subsequent behaviour of males. Specifically, upon observing that females mount males in response to their leaving females' immediate vicinity, Vasey (2002a) postulated that female-male mounting may function to focus male attention on the consortship at hand and keep males in place. While results from Chapter 2 have confirmed that male movement does prompt female-male mounting (i.e. Categories #4 and #5), subsequent male attentiveness towards females has yet to be investigated.

In Chapter 3, the mount types employed by females engaged in heterosexual and homosexual consortships could only be compared for double foot-clasp mounts, as all

other mount types were too infrequent and/or were not comparable between consortship types. While no differences were found for double foot-clasp mounts, additional analyses should be carried out to determine whether the same is true for the other mount types, particularly reclining and sitting mounts. For this to be possible, data collection that is conducted with this question in mind will have to be done in a manner that ensures that the video data lend themselves to EWMN body segment scoring. Specifically, effort will have to be made to film all mounts at horizontal and vertical angles that result in a profile view of the behaviour. This will maximize the scorability of all the captured mounts, thus allowing for an adequate and comparable frequency between consortship types.

REFERENCES

Adkins-Regan, E. (1988). Sex hormones and sexual orientation in animals. *Psychobiology, 16*, 335-347. doi:10.3758/BF03327331

Alcock, J. (1989). *Animal behavior* (4th ed.). Sunderland, MA: Sinauer Associates.

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour*, *49*, 227-267. doi:10.1163/156853974x00534

Baerends, G.P. (1975). An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In G.P. Baerends, C. Beer, & A. Manning (Eds.)*, Essays on function and evolution in behaviour* (pp. 187-227). Oxford: Clarendon Press.

Bagemihl, B. (1999). *Biological exuberance: Animal homosexual and natural diversity*. New York: St. Martin's Press.

Bateson, P., & Laland, K. (2013). Tinbergen's four questions: An appreciation and an update. *Trends in Ecology & Evolution*, *28*, 712-718. doi:10.1016/j.tree.2013.09.013

Baum, M.J. (1979). Differentiation of coital behaviour in mammals. *Neuroscience and Biobehavioral Reviews, 3*, 265-284. doi:10.1016/0149-7634(79)90013-7

Beach, F.A. (1968). Factors involved in the control of mounting behavior by female mammals. In M. Diamond (Ed.), *Perspectives in reproduction and sexual behavior: A memorial to William C. Young* (pp. 83-131). Bloomington: Indiana University Press.

Beach, F.A. (1976). Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior*, *7* 105-38. doi:10.1016/0018-506X(76)90008-8

Bielert, C., Girolami, L., Jowell, S. (1989). An experimental examination of the colourcomponent in visually mediated sexual arousal of the male chacma baboon (*Papio ursinus*). *Journal of Zoology*, *219*, 569-579. doi:10.1111/j.1469-7998.1989.tb02601.x

Buss, D.M., Haselton, M.G., Shackelford, T.K., Bleske, A.L., & Wakefield, J.C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist, 53*, 533-548. doi:10.1037/0003-066X.53.3.533

Byne, W., Tobet, S., Mattiace, L.A., Lasco, M.S., Kemether, E., Edgar, M.A., & Jones, L.B. (2001). The interstitial nuclei of the human anterior hypothalamus: An investigation of variation with sex, sexual orientation, and HIV status. *Hormones and Behavior, 40*, 86-92. doi:10.1016/S0006-8993(99)02458-0

Chapais, B., Gauthier, C., & Prud'homme, J. (1995). Dominance competition through affiliation and support in Japanese macaques: An experimental study. *International Journal of Primatology, 16*, 521-536. doi:10.1007/BF02735801

Chapais, B., Gauthier, C., Prud'homme, J., & Vasey, P.L. (1997). Relatedness threshold for nepotism in Japanese macaques. *Animal Behaviour, 53*, 1089-1101. doi:10.1006/anbe.1996.0365

Chapais, B., & Mignault, C. (1991). Homosexual incest avoidance among females in captive Japanese macaques. *American Journal of Primatology, 23*, 171-183. doi:10.1002/ajp.1350230304

Cicchetti, D.V., & Sparrow, S.S. (1981) Developing criteria for establishing the interrater reliability of specific items in a given inventory. *American Journal of Mental Deficiency, 86*, 127-137. Retrieved from http://www.ncbi.nlm.nih.gov/

Crews, D., & Moore, M.C. (1986). Evolution of mechanisms controlling mating behaviour. *Science, 231*, 121-125. doi:10.1126/science.3941893

Dagg, A.I. (1984). Homosexual behaviour and female-male mounting in mammals—a first survey. *Mammal Review*, *14*, 155-185. doi:10.1111/j.1365-2907.1984.tb00344.x

Dixson, A.F. (2012). Socio-sexual, bisexual, and homosexual behaviour. In *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and human beings* (pp. 200-231). New York: Oxford University Press.

Eaton, G.G., Worlein, J.M., Martin, T.L., & Glick, B.B. (1988). Sexual behavior of prenatally androgenized female and estrogen treated male Japanese macaques (*Macaca fuscata*) [Abstract]. *American Journal of Primatology, 14*, 419. doi:10.1002/ajp.1350140410

Enomoto, T. (1974). The sexual behavior of Japanese monkeys. *Journal of Human Evolution, 3*, 351-372. doi:10.1016/0047-2484(74)90198-5

Eshkol, N., & Wachman, A. (1958). Movement Notation. London: Weidenfeld and Fedigan, L.M. (1982). *Primate paradigms Sex roles and social bonds*. Montreal: Eden press.

Fedigan L.M., & Gouzoules, H. (1978). The consort relationship in a troop of Japanese monkeys. In D. Chivers (Ed.), *Recent advances in primatology. Vol. I. behaviour* (pp. 493-495). London: Academic Press

Fooden, J., & Aimi, M. (2005). Systematic review of Japanese macaques, *Macaca fuscata* (Gray, 1870). *Fieldiana: Zoology, 104*, 1-200. doi:10.5962/bhl.title.3500

Ford, C. S., & Beach, F. A. (1951). Homosexual Behavior. In *Patterns of Sexual Behavior* (pp. 125-143). London: Eyre & Spottiswoode.

Fruth, B. & Hohmann, G. (2006). Social grease for females? Same-sex genital contacts in wild bonobos. In V. Sommer & P.L. Vasey (Eds.), *Homosexual behaviour in animals: An evolutionary perspective* (pp. 294-315). Cambridge: Cambridge University Press.

Fukuda, F. (2004). Dispersal and environmental disturbance in Japanese macaques (*Macaca fuscata*). *Primate Reproduction, 68*, 53-69. Retrieved from http://intranet.dpz.eu

Furuichi, T., Connor, R., & Hashimoto, C. (2014). Non-conceptive sexual interactions in monkeys, apes, and dolphins. In J. Yamagiwa & L. Karczmarski (Eds.), *Primates and cetaceans: Field research and conservation of complex mammalian societies* (pp. 385-408). Tokyo: Springer. doi:10.1007/978-4-431-54523-1

Gordân, R., Narlikar, L., & Hartemink, A.J. (2010). Finding regulatory DNA motifs using alignment-free evolutionary conservation information. *Nucleic Acids Research, 38*, 1-12. doi:10.1093/nar/gkp1166

Gould, S.J. (1986). Evolution and the triumph of homology, or why history matters. *American Scientist*, *74*, 60-69. doi:10.2307/27853941

Gould, S.J. (1993). Male nipples and clitoral ripples. *Columbia: A Journal of Literature and Art*, *20*, 80-96. doi:10.2307/27853941

Gould, S.J., & Vrba, E.S. (1982). Exaptation–a missing term in the science of form. *Paleobiology*, *8*, 4-15. doi:10.2307/2400563

Gouzoules, H., & Goy, R. W. (1983). Physiological and social influences on mounting behavior of troop-living female monkeys (*Macaca fuscata*). *American Journal of Primatology*, *5*, 39-49. doi:10.1002/ajp.1350050105

Gray, H. (1918). Articulations of the trunk. In *Anatomy of the human body*. Retrieved from http://www.bartleby.com/107/72.html

Gunst, N., Leca, J.-B., & Vasey, P.L. (2013). Development of sexual and socio-sexual mounting in free-ranging juvenile male Japanese macaques (*Macaca fuscata*). *Behaviour, 150*, 1225-1254. doi:10.1163/1568539X-00003088

Gunst, N., Leca, J.-B., & Vasey, P.L. (2015). Influence of sexual competition and social context on homosexual behavior in adolescent female Japanese macaques. *American Journal of Primatology*. doi:10.1002/ajp.22369

Hanby, J.P. (1974). Male-male mounting in Japanese monkeys (*Macaca fuscata*). *Animal Behaviour, 22*, 836-849. doi:10.1016/0003-3472(74)90006-2

Hanby, J.P., & Brown, C.E. (1974). The development of sociosexual behaviours in Japanese macaques *Macaca fuscata*. *Behaviour, 49*, 152-196. doi:10.1163/156853974X00444

Harris, L.N., & Taylor, E.B. (2010). Genetic population structure of broad whitefish, *Coregonus nasus*, from the Mackenzie River, Northwest Territories: implications for subsistence fishery management. *Canadian Journal of Fisheries and Aquatic Sciences, 67*, 905-918. doi:10.1139/F10-027

Huffman, M.A., Fedigan, L.M., Vasey, P.L., & Leca, J.-B. (2012). A brief historical timeline of research on the Arashiyama macaques. In J.-B Leca, P.L. Vasey, & M.A. Huffman (Eds.), *The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 13-27). Cambridge: Cambridge University Press.

Jones, B.C., Hahn, A.C., Fisher, C.I., Wincenciak, J., Kandrika, M., Roberts, S.C., Little, A.C., DeBruine, L.M. (2015). Facial coloration tracks changes in women's estradiol. Psychoneuroendocrinology, *56*, 29-34. doi:10.1016/j.psyneuen.2015.02.021

Karlson, P., & Luscher, M. (1959) 'Pheromones': A new term for a class of biologically active substances. *Nature, 183*, 55-56. doi:10.1038/183055a0

Kawamura, S. (1958). Matriarchal social ranks in the Minoo-B Troop: A study of the rank system of Japanese monkeys. In K. Imanishi & S. Altmann (Eds.), *Japanese Monkey*s (pp. 105-112). Atlanta: Emory University.

Kendrick, K.M., & Dixson, A.F. (1986) Anteromedial hypothalamic lesions block proceptivity but not receptivity in the female common marmoset (*Callithrix jacchus*). *Brain Research, 375*, 221–229. doi:10.1016/0006-8993(86)90741-9

Koyama, N. (1967). On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. *Primates*, *8*, 189-216. doi:10.1007/BF01731037

Koyama, N.F. (2003). Matrilineal cohesion and social networks in *Macaca fuscata. International Journal of Primatology, 24,* 797-811. doi:10.1023/A:1024676705433

Landis, R.J., & Koch, G.G. (1977). The measurement of observer agreement for categorical data. *Biometrics, 33*, 159-174. doi:10.2307/2529310

Leca, J.-B., Gunst, N., & Vasey, P.L. (2014a). Development of sexual behavior in free-ranging female Japanese macaques. *Developmental Psychobiology, 56*, 1199-1213. doi:10.1002/dev.21201

Leca, J.-B., Gunst, N., Ottenheimer Carrier, L., & Vasey, P.L. (2014b). Inter-group variation in non-conceptive sexual activity in female Japanese macaques: Could

it be cultural? *Animal Behavior and Cognition, 1,* 387-409.
doi:10.12966/abc.08.12.2014

Leca, J.-B., Gunst, N., & Vasey, P.L. (2014c). Male homosexual behavior in a free-
ranging all-male group of Japanese macaques at Minoo, Japan. *Archives of
Sexual Behavior, 43,* 853-861. doi:10.1007/s10508-014-0310-6

Leca, J.-B., Gunst, N., & Vasey, P.L. (2014d). Comparative development of heterosexual
and homosexual behaviors in free-ranging female Japanese macaques. *Archives
of Sexual Behavior.* doi:10.1007/s10508-014-0437-5

Leca, J.-B., Gunst, N., Huffman, M. A., & Vasey, P.L. (2015). Effect of female-biased
sex ratios on female homosexual behavior in Japanese macaques: Evidence for
the "bisexual preference hypothesis". *Archives of Sexual Behavior.*
doi:10.1007/s10508-015-0522-4

Morris, D. (1955). The causation of pseudofemale and pseudomale behaviour: A further
comment. *Behaviour, 8*, 46-56. doi:10.1163/156853955X00148

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of
small samples often leads to incorrect P values: Examples from Animal
Behaviour. *Animal Behaviour, 56*, 256-259. doi:10.1006/anbe.1998.0756

Nakagawa, N., Matsubara, M., Shimooka, Y., & Nishikawa, M. (2015). Embracing in a
wild group of Yakushima macaques (*Macaca fuscata yakui*) as an example of
social customs. *Current Anthropology*, *56*, 104-120. doi:10.1086/679448

Nigi, H. (1975). Menstrual cycle and some other related aspects of Japanese monkeys
(*Macaca fuscata*). *Primates, 16*, 207-216. doi:10.1007/BF02381418

O'Neill, A.C., Fedigan, L.M., & Ziegler, T.E. (2004a). Relationship between ovarian
cycle phase and sexual behavior in female Japanese macaques (*Macaca fuscata*).
American Journal of Physical Anthropology, 125, 352-362.
doi:10.1002/ajpa.20024

O'Neill, A.C., Fedigan, L.M., & Ziegler, T.E. (2004b). Ovarian cycle phase and same-sex
mating behavior in Japanese macaque females. *American Journal of
Primatology, 63*, 25-31. doi:10.1002/ajp.20034

Palastanga, N., & Soames, R. (2012). The trunk and the neck. In *Anatomy and human
movement: Structure and function* (6th ed.) (pp. 405-542). Edinburgh: Elsevier.

Pellis, S.M, Blundell, M.A, Bell, H.C., Pellis, V.C., Krakauer, A.H., & Patricelli, G.L.
(2013). Drawn into the vortex: The facing-past encounter and combat in lekking
male greater sage-grouse (*Centrocercus urophasianus*). *Behaviour, 150*,1567-
1599. doi:10.1163/1568539X-00003110

Reinhart, C.J., Pellis, V.C., Thierry, B., Gauthier, C.-A., VanderLaan, D.P., Vasey, P.L., & Pellis, S.M. (2010). Targets and tactics of play fighting: Competitive versus cooperative styles of play in Japanese and Tonkean macaques. *International Journal of Comparative Psychology*, *23,* 166-200. Retrieved from http://escholarship.org

Roselli, C.E., Larkin, K., Resko, J.A., Stellflug, J.N., & Stormshak, F. (2004). The volume of a sexually dimorphic nucleus in the ovine medial preoptic area/anteriorhypothalamus varies with sexual partner preference. *Endocrinology, 45*, 478-83. doi:10.1210/en.2003-1098

Schaefer, H., & Ruxton, G. (2012). By-product information can stabilize the reliability of communication. *Journal of Evolutionary Biology*, *25*, 2412-2421. doi:10.1111/jeb.12020

Scott-Phillips, T.C., Dickins, T.E., & West, S.A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspectives on Psychological Science*, *6*, 38-47. doi:10.1177/1745691610393528

Seeley, T.D. (1995). *The wisdom of the hive: The social physiology of honey bee colonies*. Cambridge, MA: Harvard University Press.

Shimada, M. (2006). Social object play among young Japanese macaques (*Macaca fuscata*) in Arashiyama, Japan. *Primates, 47*, 342-349. doi:10.1007/s10329-006-0187-7

Siegel, S. & Castellan, N.J. Jr. (1988). *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill. doi:10.4135/9781412961288

Smith, P.K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. *Behavioral and Brain Sciences*, *5*, 139-184. doi:10.1017/S0140525X0001092X

Takahata, Y. (1980). The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates, 21,* 303-329. doi:10.1007/BF02390462

Takenoshita, Y. (1998). Male homosexual behaviour accompanied by ejaculation in a free-ranging troop of Japanese macaques (*Macaca fuscata*). *Folia Primatologica, 69*, 364-367. Retrieved from http://www.ipce.info

Tasumi, M. (1969). Senile features in the skeleton of an aged a Japanese monkey. *Primates, 10*, 263-272. doi:10.1007/BF01730347

Thierry, B., Iwaniuk, A.N., & Pellis, S.M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology, 106*, 713-728. doi:10.1046/j.1439-0310.2000.00583.x

Thomsen, R., & Soltis, J. (2004). Male masturbation in free-ranging Japanese macaques.

International Journal of Primatology, 25, 1033-1041.
doi:10.1023/B:IJOP.0000043350.75897.89

Tinbergen, N. (2963). On aims and methods in Ethology. Zeitschrift für Tierpsychologie, *20*, 410-433. doi:10.1111/j.1439-0310.1963.tb01161.x

VanderLaan, D.P., Pellis, S.M., & Vasey, P.L. (2012). A theoretical model of the development and evolution of non-conceptive mounting behaviour in Japanese macaques. In J.-B. Leca, M.A. Huffman, & P.L. Vasey (Eds.) *The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 187-203). Cambridge: Cambridge University Press.

Vasey, P.L. (1995). Homosexual behavior in primates: A review of evidence and theory. *International Journal of Primatology*, *16*, 173-204. doi:10.1007/BF02735477

Vasey, P.L. (1996). Intervention and alliance formation between female Japanese macaques, *Macaca fuscata*, during homosexual consortships. *Animal Behaviour, 52*, 539-551. doi:10.1006/anbe.1996.0196

Vasey, P. L. (1998). Female choice and inter-sexual competition for female sexual partners in Japanese macaques. *Behaviour, 135*, 579-597. Retrieved from http://www.jstore.org

Vasey, P.L. (2002a). Same-sex sexual partner preference in hormonally and neurologically unmanipulated animals. *Annual Review of Sex Research, 13*, 141-179. doi:10.1080/10532528.2002.10559804

Vasey, P.L. (2002b) Sexual partner preference in female Japanese macaques. *Archives of Sexual Behavior, 31*, 45-56. doi:10.1023/A:1014079117864

Vasey, P.L. (2004a). Sex differences in sexual partner acquisition, retention, and harassment during female homosexual consortships in Japanese macaques. *American Journal of Primatology, 64*, 397-409. doi:10.1002/ajp.20088

Vasey, P. L. (2004b). Pre- and post-conflict interactions between female Japanese macaques during homosexual consortships. *International Journal of Comparative Psychology, 17,* 351-359. Retrieved from http://escholarship.org

Vasey, P.L. (2006). The pursuit of pleasure: Homosexual behavior, sexual reward, and evolutionary history in Japanese macaques. In P.L. Vasey & V. Sommer (Eds.), *Homosexual behavior in animals: An evolutionary perspective* (pp. 191-219). Cambridge: Cambridge University Press.

Vasey, P.L. (2007). Function and phylogeny: The evolution of same-sex sexual behaviour in primates. *Journal of Psychology & Human Sexuality*, *18*, 215-244. doi:10.1300/J056v18n02_07

Vasey, P.L., Chapais, B., & Gauthier, C. (1998). Mounting interactions between female Japanese macaques: Testing the influence of dominance and aggression. *Ethology*, *104,* 387-398. doi:10.1300/J056v18n02_07

Vasey, P.L. & Duckworth, N. (2006). Sexual reward via vulvar, perineal, and anal stimulation: A proximate mechanism for female homosexual mounting in Japanese macaques. *Archives of Sexual Behavior, 35*, 523-532. doi:10.1007/s10508-006-9111-x

Vasey, P.L., & Duckworth, N. (2008). Female-male mounting in Japanese macaques: The proximate role of sexual reward. *Behavioural Processes*, *77*, 405-407. doi:10.1016/j.beproc.2007.07.004

Vasey, P.L., Foroud, A., Duckworth, N., & Kovacovsky, S.D. (2006). Male-female and female-female mounting in Japanese macaques: A comparative study of posture and movement. *Archives of Sexual Behavior, 35*, 117-129. doi:10.1007/s10508-005-9007-1

Vasey, P.,L. & Gauthier, C. (2000). Skewed sex ratios and female homosexual activity in Japanese macaques: An experimental analysis. *Primates*, *41,* 17-25. doi:10.1007/BF02557458

Vasey, P.L. & Pfaus, J. (2005). A sexually dimorphic hypothalamic nucleus in a macaque species with frequent female-female mounting and same-sex sexual partner preference. *Behavioural Brain Research*, *157*, 265-272. doi:10.1016/j.bbr.2004.07.005

Vasey, P.L. & Reinhart, C.J. (2009). Female homosexual behavior in a new group of Japanese macaques: Evolutionary implications. *Laboratory Primate Newsletter, 48*, 8-10. Retrieved from http://www.brown.edu/

Vasey, P.L. & Sommer, V. (Eds.) (2006). *Homosexual behaviour in animals: An evolutionary perspective*. Cambridge University Press, Cambridge.

Vasey, P.L., & VanderLaan, D.P. (2012). Is female homosexual behaviour in Japanese macaques truly sexual? In J.-B Leca, M.A. Huffman, & P.L. Vasey (Eds.), *The monkeys of stormy mountain: 60 years of primatological research on the Japanese macaques of Arashiyama* (pp. 153-172). Cambridge: Cambridge University Press.

Waitt, C. Gerald, M.S., Little, A.C., & Kraiselburd, E. (2006). Selective attention towards female secondary sexual color in male rhesus macaques. *American Journal of Primatology, 68*, 738-744. doi:10.1002/ajp.20264

Wallen, K. (2001). Sex and context: Hormones and primate sexual motivation. *Hormones and Behavior, 40*, 339-357. doi:10.1006/hbeh.2001.1696

Whishaw, I.Q., & Pellis, S.M. (1990). The structure of skilled forelimb reaching in the rat: A proximally driven movement with a single distal rotatory component. *Behavioural Brain Research, 41*, 49-59. doi:10.1016/0166-4328(90)90053-H

Wickler, W. (1967). Socio-sexual signals and their intra-specific imitation among primates. In D. Morris (Ed.), *Primate ethology* (pp. 69-79). Chicago: Aldine.

Wolfe, L. D. (1979a). Behavioural patterns of estrous females of the Arashiyama West troop of Japanese macaques (*Macaca fuscata*). *Primates, 20*, 525-534. doi:10.1007/BF02373434

Wolfe, L. D. (1979b). Sexual maturation among members of a transported troop of Japanese macaques (*Macaca fuscata*). *Primates*, *20*, 411-418. doi:10.1007/BF02373392

Wolfe, L. D. (1984). Japanese macaque female sexual behavior: A comparison of Arashiyama East and West. In M.F. Small (Ed.), *Female primates: Studies by women primatologists* (pp. 141-157). New York: Allan R. Liss.

Wolfe, L.D. (1986). Sexual strategies of female Japanese macaques (*Macaca fuscata*). *Human Evolution, 1*, 267-275. doi:10.1007/BF02436584

Wundram, I. (1979). Nonreproductive sexual behavior: Ethological and cultural considerations. *American Anthropologist, 81*, 99-103. doi:10.1525/aa.1979.81.1.02a00140

Yamagiwa, J., & Hill, D. A. (1998). Intraspecific variation in social organization of Japanese macaques: Past and present scope of field studies in natural habitats. *Primates, 39*, 257-227. doi:10.1007/BF02573076

APPENDIX
Qualitative Description of Male-Initiated Category #4 and #5 Mounts

Category #4 mounts

Instance 1: The female and male are sitting chest-to-back (respectively) and touching one another, with the female holding her arms around the male's torso in a resting state. The male gets up, with the female still embracing his torso, and a female-male mount occurs. During the mount, the male is stationary and leaning against a fence, standing on his hind legs only. Upon dismounting, both individuals remain within 1 monkey length of their mounting location, still touching.

Instance 2: The female and male are sitting side-to-side and in body contact. The male leans his torso forward slightly, but still remains sitting. The female then turns around and gets up, followed by the male getting up. The female grasps the male, and a female-male mount occurs, with the male remaining stationary during the mount. Upon the dismount, both individuals sit down within 1 monkey length of the mounting location, still touching.

Instance 3: The female is lying on her side and being groomed by the male, who is sitting behind her. The male turns to get up, prompting the female to get up from her lying position. The female grasps and mounts the male just as he became fully standing. Once she has mounted, the male gets up on his two hind legs for approximately 1 s, and then begins to walk. With the female still on his back, the male walks approximately 15 monkey lengths. Upon the dismount, both individuals sit down less than 1 monkey length of the mounting location, still in body contact.

Instance 4: The male is sitting behind and in body contact with the female, his chest in contact with her back. The male leans his torso to the side. The female then begins turning and reaching for the male, followed by the male moving to stand up. The female grasps and mounts the male, who moves 1 monkey length in horizontal distance as he is being mounted. Upon the dismount, both individuals sit down less than 1 monkey length of the mounting location, still in body contact.

Instance 5: The male is sitting behind the female, his chest within an arm's length away from her back. The female vocalizes and turns her head slightly to the male. In turn, the male begins shifting his body to stand. The female then turns her torso and grabs and mounts the male. The male remains stationary during the mount. Upon the dismount, both individuals sit down less than 1 monkey length of the mounting location, still in body contact.

Category #5 mounts

Instance 1: The female and male are sitting and in body contact. The male intensely gazes at something out of frame, then quickly gets up and runs in the direction of his gaze. The female attempts but fails to grab the male as he is getting up, and proceeds to chase him. After 4-5 monkey lengths of running, the female catches up to and grasps the male's hindquarterss, and she begins mounting him. Once she has fully mounted (i.e. her feet are clasped around the male's ankles), the male becomes stationary. Upon the dismount, both individuals sit down less than 1 monkey length of the mounting location, still in body contact.

Instance 2: The female is scaling the walls of the tourist feeding area and begging for food, with the male sitting on the ground approximately 1 m below her. The male gets up and begins walking away when the female begins vocalizing towards the male. The male

turns around while continuing to walk and looks at the female. The female then descends from the wall and runs towards the male, still vocalizing. The male begins to sprint away from the female, but stops running after approximately 4 monkey lengths. The female quickly catches up to the male, grabbing and mounting him. Upon dismount, both sit down within the same area that the mounting occurred, in body contact with one another. Instance 3: Both the male and female are scaling the walls of the tourist feeding area and begging for food approximately 5 monkey lengths away from one another. The male descends from the wall and leaves the frame. The female continues to beg, looking around regularly. Approximately 1 minute after the male's departure from frame, the female begins to vocalize while looking around. She descends from the wall and runs towards the male, still vocalizing. When the male re-enters the frame (via the camera following the female's movement), he is standing quadrupedally, stationary, and approximately 9 monkey lengths away from the female's original begging position. She mounts the already-standing male, who remains still throughout the mount. Upon dismount, both sit down within the same area that the mounting occurred, in body contact with one another. I interpreted this mounting sequence as being a delayed reaction to male departure.

Instance 4: The male and female are sitting back-to-back within arm's reach of one another. The male stands, turns towards the female's direction and walks by the female, intensely gazing at her as she walks by. The female grasps and mounts the male when he arrives in front of her, and the male stops moving. During the mount, the male remains still and vocalizes. Upon dismount, both individuals sit down within the same area that the mounting occurred, in body contact with one another.